CHANGES IN ARABLE WEED COMMUNITIES OVER THE LAST 100 YEARS

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General Introduction

Historical background

Arable weeds, also known as segetal flora, are plants whose lifecycle is attuned to the rhythm of sowing and harvesting (Scholz, 1996). They can be defined as plants which preferably grow in cultivated fields, but are not intentionally sown or planted there. In Europe, arable weeds evolved mainly from Mediterranean plants during the domestication and development of cereal crops during the last 5000 years (Holzner & Immonen, 1982). After AD 1500, new crop species were introduced from the new world. These species were maize, potatoes and tomatoes, for example. The weeds associated with those crops were co-introduced, which led to an even richer arable flora (Holzner & Immonen, 1982). By the beginning of the twentieth century, a very rich arable flora had been assembled in Central Europe. It consisted of indigenous ruderal plants, old elements from southern Europe and the Mediterranean Basin, and newer elements from the Americas. Over thousands of years, the weed species evolved functional traits that allow them to survive in a regularly disturbed habitat. Some species mimic the crop they are associated with (Barrett, 1983; Landolt *et al.*, 2010; Gunton *et al.*, 2011). Some seeds of arable weeds have the size and shape of the crop they are associated with, like *Agrostemma githago* L. which is associated with cereals. Others have a similar growth-form as the crop species to avoid being weeded such as *Echinochloa crus-galli* L. or *Centaurea cyanus* L.. Most weed species have an annual life cycle. This allows the plant to reproduce in the small timespan between the sowing and harvesting of the crop species. Another possibility for the plant is to grow rhizomes that are able to build new shoots after ploughing. Yet an alternative survival strategy of arable weed species is to grow seeds capable of germinating after relatively long time periods (Thompson *et al.*, 1998). In general, up to 40% of the seeds of weed species can still germinate after 50 years of dormancy (Wäldchen *et al.*, 2005). However, the loss of seeds is higher in light soils than in heavy soils (Lutman *et al.*, 2002) while changing from conventional to organic farming increases seed density as well as the number of species present with seeds in the seed bank

(Albrecht, 2005). After abandonment or conversion to grassland, seed density of weed species decreases by 40% in 6 years (Mrotzek & Schmidt, 1993; Albrecht, 2005; Albrecht & Auerswald, 2009).

On traditionally managed arable fields a multitude of species can coexist. This species richness is recorded with a relevé and is affected by the date of the respective relevé (Lososová *et al.*, 2004; Pysek *et al.*, 2005). As even in the short-lived species of arable weeds, the date of germination is not the same for all species to minimize interspecific competition. Hence, not all species potentially present at the respective field can be detected at all points in time. Not all weed species grow with every crop species sown on the field. There are species like *Centaurea cyanus* L., *Consolida regalis* Gray. or *Agrostemma githago* L. that mostly grow in cereal fields, while *Fumaria officinalis* L. or *Aethusa cynapium* L. grow mainly in root crops (Delarze & Gonseth, 2008). Cereal crops usually harbour more species per area as root crops (Delarze & Gonseth, 2008). Additionally, the higher the management intensity on a field, the lower the weed species richness (Hyvönen *et al.*, 2003; Lososová *et al.*, 2004; Baessler & Klotz, 2006). Also climatic conditions like altitude (Lososová *et al.*, 2004) or mean temperature (Pysek *et al.*, 2005; Glemnitz *et al.*, 2006) can influence the species richness of a field. The structure of the surrounding environment is yet another important factor influencing the species richness of the arable flora. The more heterogeneous the landscape is around a field, the higher the respective species number is in the field (Baessler & Klotz, 2006). The diversity of species and traits ensures the functioning of the ecosystem and the services resulting out of them (Franke *et al.*, 2009; Isbell *et al.*, 2011). These services include food-resources for birds that live in agricultural habitats (Hole *et al.*, 2005), food and shelter for beneficial organisms like wild bees and ladybugs (Isaacs *et al.*, 2008) as well as protection from erosion (Pimentel *et al.*, 1995) and a recreational effect for persons taking a walk in a colourful landscape (Junge *et al.*, 2011).

Since the 1920s, many studies exploring the plant communities in arable fields have been published from all over Europe (Mann, 1939; Ellenberg, 1950; Holzner, 1978). They led to many

different described plant sociological units that distinguish plant communities of different crop- and soil-types. Those plant sociological units are defined by certain species that are characteristic for the growing conditions in those habitats and which seldom grow in other habitats (Ellenberg, 1950, 1956). Therefore, it is possible to assign relevés to these sociological units long after their recording. In Switzerland, five major studies on the arable flora were conducted (Volkart, 1933; Buchli, 1936; Salzmann, 1939; Brun-Hool, 1963; Waldis, 1986). They were geographically distributed across the whole country and also explored different farming practices. Volkart (1933) conducted his study on arable fields in the alpine valleys of Switzerland. He recorded 893 relevés between 1927 and 1945. He showed differences of the arable communities among the diverse valleys in the Swiss Alps. Buchli (1936) recorded 272 relevés in areas with a three-field crop rotation system. His plots were distributed across the cantons Aargau, Schaffhausen and Zürich. Based on these plots he showed the peculiarity of the arable weed communities in this region based on soil-samples and climatic conditions. Salzmann (1939) showed the influence of changing between crops and leys on the same field on arable weed species. Additionally he tried to find the characteristic species for this management system (Kleegraswirtschaft) in Switzerland. Based on soil samples he drew conclusions about their ecology such as which species grow on which soil types. He recorded 344 relevés from the plateau of the cantons Bern, Fribourg and Luzern in the years 1935 and 1936. Brun-Hool (1963) recorded over 1000 relevés under different management practices in the north-western part of Switzerland between 1954 and 1958. Those relevés were assigned to 16 communities of which some can be found across Switzerland. Waldis (1986) recorded over 2000 relevés in the canton of Valais between 1974 and 1980. He classified those relevés into 23 plant-sociological communities based on region, soil properties and crop type. The relevés of all five authors are included in the vegetation database of Agroscope. It currently contains around 35’000 vegetation relevés on agricultural land between 1886 and present days. The about 4’500 relevés from the above mentioned authors recorded on arable land in the years 1927 to 1980 in different Swiss regions are shown in Fig. 1.

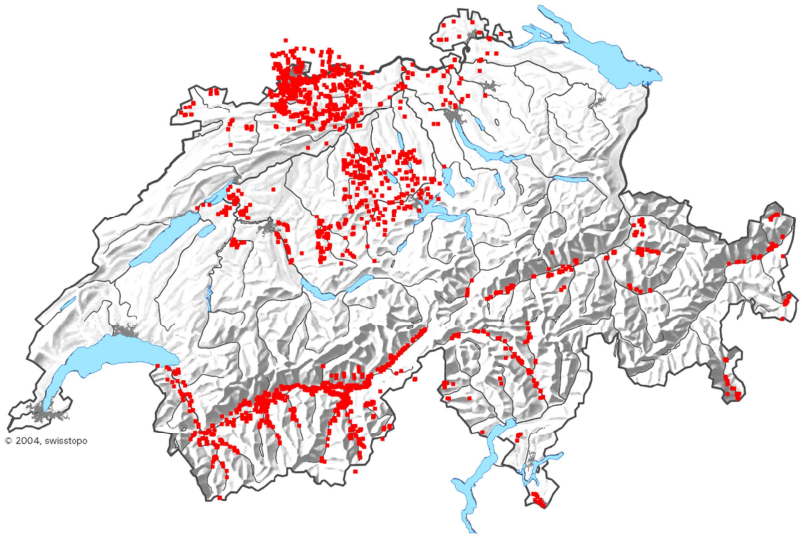

Fig. 1**: Distribution of historical vegetation relevés of crop fields in Switzerland and adjacent regions (geodata © swisstopo)**

Changes in agricultural practice

During the last 100 years, rapid changes in agricultural practices had a high impact on arable weeds. In traditional farming, the fields were small and had complex landscapes surrounding them as farms were not specialised in a certain management type (Bouma *et al.*, 1998; Chamberlain *et al.*, 2000). In Europe, farming practice changed from manual labour supported by animal power to highly mechanised processes. It is today characterised by high input of fertilizers and pesticides (Robinson & Sutherland, 2002; Herzog *et al.*, 2006). This results in minimal intra-crop competition for nutrients and a reduction of infestation by noxious weeds. This again allows farmers to grow crop plants in higher densities and achieve higher yields, but it also negatively affects the accompanying arable flora (Robinson & Sutherland, 2002). The higher densities of crop species due to higher amounts of nutrients in the soil hinders light to penetrate to the ground. This lack of light is one of the key factors for the decline of biodiversity in agricultural habitats because many arable species cannot thrive under low-light conditions (Hautier *et al.*, 2009). Additionally, as weed species already growing on the field die after the application of herbicides, they will not reproduce. Therefore, the seedbank in the soil becomes depleted and the affected species will be lost from the community (Armengot *et*

al., 2011). Contributing to the decline in species, the season in which cereals are sown has changed from spring to autumn. This makes it difficult for weeds that germinate in spring, as they have to compete for light with crop species being already tall and established (Hald, 1999). Moreover, as crop seed cleaning has become more efficient, seeds of arable weeds are no longer spread on fields via crop seeding (Van Elsen, 1994). As a consequence of all these changes, over 300 arable weeds species in Switzerland are presently rare or extinct and therefore red listed (Moser *et al.*, 2002). Depending on the country, up to 77% of the arable flora is threatened in Europe and including all European countries 582 species are threatened (Storkey *et al.*, 2012).

On the other hand, there are also some arable weed species that managed to adapt to the rapid changes. Many studies showed that species can become resistant to herbicides if these are applied regularly (Holt & Lebaron, 1990). Other species that already have an adaptation to the new circumstances benefit from niches that become unoccupied as other species disappear (Grime, 2002). Therefore, changes happen not only due to loss but also due to spread and invasion of new species (Pàl, 2004; Májeková *et al.*, 2010). A meta-study for Central Europe shows a reduction of species per field of 20 to 50% for the period from 1950 to 1990 (Albrecht and Bachthaler, 1990). They noted that most threatened species were already rare in the 1950-ies. Several recent case studies from Europe have found a higher overall species richness in present days than 20 to 65 years earlier (Sutcliffe & Kay, 2000; Hyvönen *et al.*, 2003; Šilc & Čarni, 2005; Baessler & Klotz, 2006; Dessaint *et al.*, 2007). However, they did not analyse if this increase was due mainly to neophytes and pesticide-resistant species as shown by Otte *et al.* (2006) for Germany. The mean species number and the mean coverage of species in individual fields decreased in the majority of cases (Albrecht & Bachthaler, 1990; Šilc & Čarni, 2005; Baessler & Klotz, 2006). In Oxfordshire (GB) species that had been rare in the previous survey were hardly present 40 years later (Sutcliffe & Kay, 2000).

To counteract the loss of biodiversity in agricultural landscapes in general and of arable weeds in particular, several measures were taken across Europe in the 1980s. To promote arable weed species, many countries introduced agri-environmental schemes like flower strips or set-aside land (ECC Regulation 797/85, Eidgenossenschaft, 2014). Around the same time, organic farming was becoming more wide-spread. Organic farming does not allow the use of herbicides and industrial fertilizers and has a positive effect on plant diversity (Bengtsson *et al.*, 2005; Hole *et al.*, 2005). The agri-environmental schemes also have a positive effect on plant diversity in agricultural habitats (Kleijn *et al.*, 2006; Marshall *et al.*, 2006). However, the agri-environmental schemes on arable land were not adopted by the farmers to a sufficiently large extent. Today, only 2% of all registered areas with agri-environmental schemes in Switzerland are on arable fields. This means that only 0.6% of the total arable area is managed as promotion-areas for biodiversity (Eidgenossenschaft, 2014, Art. 55) although about 10% would be necessary to sufficiently promote the arable flora (BLW, 2013; Guntern *et al.*, 2013). In Switzerland, not only changes in farming practice threaten the diversity of arable weed species but also the decrease in distribution of available habitat. From 1990 to 2012 the amount of arable area declined from 316'000 ha (7.7% of the total area of Switzerland) to 270'000 ha (BFS, 2013) due to conversion from arable to dairy farming. This conversion from arable fields to grassland often happens in marginally profitable areas where plant diversity is still high (MacDonald *et al.*, 2000). In these regions, the conservation of arable weeds is even more important and urgent.

Community ecology and phylogeny

The evolution of species is based on the modification of heritable characteristics (Darwin, 1859). Some characteristics and traits may change due to strong enough environmental variables so the species is afterwards better adapted. If many of those changes take place in a sub-population, this can lead to speciation (Sibly, 1995). A way to picture the result of this process is the phylogenetic tree. This tree depicts the relatedness among the species, usually including the time component of

the processes (Webb & Donoghue, 2005). Phylogenetic trees were formerly inferred from the morphological features of the included species. In recent times this approach has been replaced by molecular methods that base on sequences of DNA or proteins (Rannala & Yang, 1996). These trees can be used to link evolutionary processes to other fields in biology such as behaviour (Thierry *et al.*, 2000) or conservation (Agapow *et al.*, 2005). The integration of phylogenetic findings into community ecology however has long been neglected (Webb *et al.*, 2002). In the last decade this integration was initiated with a focus on the processes regulating the assembly of plant communities (Webb, 2000a; Cavender-Bares *et al.*, 2004; Silvertown *et al.*, 2006; Whitfeld *et al.*, 2012). Earlier studies mentioned limiting similarity as an important community assembly criterion, whereas more recently the focus shifted to a duality of processes: filtering or competition. (Pavoine & Bonsall, 2011). Habitat filtering is the result of strong selective environmental variables, allowing only species with the necessary adaptations to survive. Competition means that not all species that have the same requirements for the habitat can co-exist in the same community. If competition between the species controls their assembly, then they should be phylogenetically over-dispersed. On the other hand, if it's environmental stress or habitat filtering, as for example the presence of generalist enemies controlling the species assembly, then phylogenetic clustering would be predicted (Cavender-Bares *et al.*, 2009). An overdispersed or clustered community means that co-occurring species are more closely or more distantly related than in a random community, respectively (Emerson & Gillespie, 2008). Thus, analysing the phylogenetic structure gives us insight on the underlying ecological processes that formed the studied communities (Webb, 2000b).

To measure phylogenetic structure several metrics can be used (Webb, 2000a). In this thesis, I used NRI and NTI measures. They are appropriate to compare communities from different habitats. The NRI is a comparison of the mean phylogenetic distance (MPD) of a random community consisting of species from the same phylogenetic tree as the observed communities and the observed

community. High positive values point to a phylogenetically clustered community, while low or negative values indicate that the species in the community are evenly spread or overdispersed across the phylogenetic tree. The MPD is the average of the sum of all pairwise distances among all pairs of species in the community. This distance is calculated by summing up the branch lengths between the two species in the phylogenetic tree. By comparing an observed and a random community, NTI measures the extent of terminal clustering on this tree. It is calculated by measuring the average minimal branch length between taxa in the observed and in the random community. Afterwards the mean net relatedness distance (MNRD) is determined. As in the NRI, low or negative values of these indices indicate overdispersion of taxa, while high positive values indicate clustering of taxa across the phylogeny.

If the phylogenetic structure of a community is known, it is possible to link these patterns to the plant functional traits present in the community. These are attributes of plants that define their life-history and growth form characteristics as well as environmental requirements. Many plant functional traits for the species present in Switzerland are listed in the Flora Indicativa (Landolt *et al.*, 2010). The combination of these traits shows to which environmental conditions a species is adapted (Losos, 2008). As closely related species share a common ancestor, they tend to have similarities in habit and constitution (Darwin, 1859). Therefore, the same mechanisms of filtering and competition apply for the assemblage of traits in a community (Kraft *et al.*, 2007). When, additionally, a majority of the species share a particular combination of traits it is possible to conclude what constitutes these filters, based on the present traits (Pavoine *et al.*, 2011).

Aim

As arable weeds are among the most threatened species groups of Switzerland, it is important to know how these communities have changed over the last decades. Especially since the arable weeds ensure the functioning of an ecosystem that covers 10% of the terrestrial surface of the world and on

which mankind depends to produce most of its food (Altieri, 1999; Klein Goldewijk *et al.*, 2007). Therefore, the following main questions arose:

1. How did the arable flora change in Switzerland over the last 90 years? (Chapter 2)
2. How did the phylogenetic structure of communities in agricultural habitats in Switzerland change from historic to contemporary relevés? (Chapter 3)
3. Would it be possible to re-establish populations of threatened arable species on abandoned arable fields in the Swiss Alps? (Chapter 4)

The vegetation database of Agroscope provides an excellent baseline to monitor changes in the Swiss flora. It is important to set this study into a bigger context. Hence, I was also interested in how the arable flora has changed in other European countries. For this purpose, as a pre-study, I reviewed the literature on studies on the same topic conducted in Europe (Chapter 1). Additionally, I also wanted to see which changes have happened on the level of plant functional traits and put these results in relation to changes in agricultural practice and species loss. To answer these questions I did a re-visiting study. On arable fields for which historical vegetation data was available and that were still cropped I recorded the vegetation. On arable fields that were converted to grassland I took soil samples to look for arable weeds still present in the seedbank, sometimes over 30 years after conversion. This thesis will be the base for identifying criteria for arable weed promotion areas and proposing selected plots for the establishment of such areas. Furthermore, recommendations of measures needed to preserve and promote the arable flora are included in the thesis.

Change across Europe

The literature review yielded 32 studies including 53 datasets that dealt with the change of the average weed species number per relevé in European countries in the last century. The geographical extent of the studies reached from Spain to Norway. The studies were carried out at different points in time, in different countries and a variety of crop types, comparing different time periods. Not

surprisingly, all those studies yielded different results on the extent and direction of the observed change. However, I wanted to get an overview across Europe. To that end, I performed a meta-analysis to show the changes in the arable flora across Europe in the last century. Meta-analysis is a useful tool to summarise results across many different studies (Hedges *et al.*, 1999). It uses a measure of the outcome of the specific study (effect size) with the variation around its mean as a weighting factor to find the mean effect size of all studies together (Borenstein *et al.*, 2009). Therefore, they have the potential to be more informative about general trends than a single study.

The meta-analysis yielded an overall mean effect size (log response ratio; lnRR) of the 53 datasets over the average species number per plot of lnRR = -0.208. In other words, the average number of arable species per plot declined by about 20% since 1939. There was no significant influence of crop type, geographic location, precipitation or study design on the decrease in average species number per plot. Hence, this decline is a general trend across Europe and not dependent on country or crop type studied but likely due to changes in agricultural practice. Since the 1980s the average species number per plot increased again in northern European countries. The total species number per study decreased across all included studies by about 7%. On average 18.5 species per study were lost and 15.2 species were gained.

The increase in mean number of species per plot since 1980 might be due to the introduction of agri-environmental schemes as well as to an increase of organic farming since the 1980's. The available data implies, that most arable plant species which have increased in frequency need a high nutrient-level in the soil, are herbicide resistant or are listed as neophytes. This indicates that rather the weeds problematic for agriculture (e.g. with a negative influence on the yield) have increased in number and not the rare and threatened traditional arable weeds. This finding is not surprising given that arable land faces high nutrient and herbicide inputs (Robinson & Sutherland, 2002); an agricultural practice that seems to favour problematic weeds.

With this meta-analysis it is not possible to confirm agri-environmental schemes to be the sole factor influencing this increase. Yet, it is in line with other studies stating a positive effect of agri-environmental measures on species richness (Kleijn & Sutherland, 2003; Bengtsson *et al.*, 2005; Aviron *et al.*, 2008). The target species of the agri-environmental schemes would ideally be a set of threatened species, adapted to low nutrient input, which produce a lot of pollen, nectar and seeds. Such species would not only help to maintain a high plant diversity but also nourish birds and beneficial organisms such as bees and green lacewings. These beneficial organisms could help to maintain high yields of insect-pollinated crops and lower the input of chemical pest controls (Isaacs *et al.*, 2008).

The results of this meta-analysis allowed to put the result of the following study that was conducted in Switzerland into a larger context.

Change in Switzerland

Study region

The study sites were distributed between 245 m and 1670 m above sea level across all six biogeographic regions of Switzerland: Jura (JU), Midlands (ML), northern Alps (NA), southern Alps (SA), eastern central Alps (EZA) and western central Alps (WZA, Gonseth *et al.*, 2001). They have a latitudinal range of 214 km and a longitudinal range of 269 km. Mean annual temperature across those regions varies between 5.5° C and 10.5° C, and mean annual rainfall varies between 545 mm and 1900 mm (MeteoSchweiz, 2013). The sampled plots for the seedbank study consisted of meadows from the bottom of the valley up to about mid-slope of the adjacent mountains. The meadows on the slope were mostly growing on old, traditionally built terraces. The soils had a mostly shallow to intermediate depth with a medium to high proportion of stones. The visited locations are shown in Fig. 2.

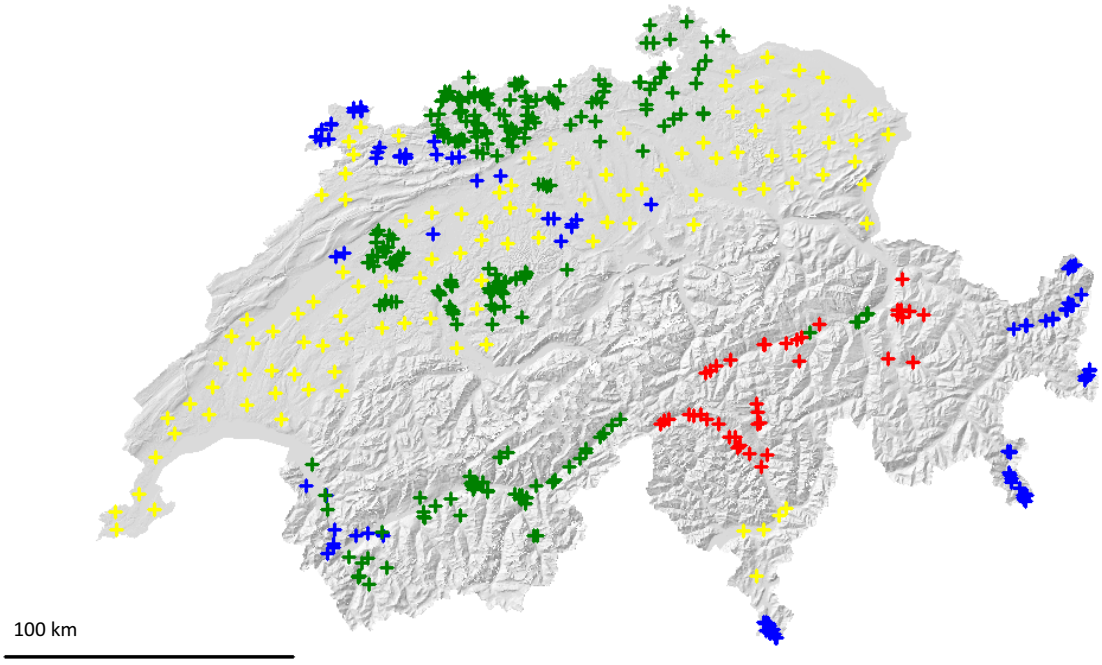

Fig. 2: **All visited locations in 2011 and 2012. Green: re-visited locations 2011; blue: re-visited locations 2012; red: locations of soil samples (2011); yellow: additional vegetation relevés (2012; geodata © swisstopo).**

A short summary of the methods used

Localisation

Many older vegetation relevés had no spatial coordinates. In order to find the right spot to record the re-survey, the location of the historical relevés had to be identified. To do this, I depended on the original historical references in combination with spatial analysis in ArcGIS (ESRI). The fieldname given in the historic relevé was searched in the historic map. Afterwards an analysis on the combination of slope, altitude and exposition with a more precise description of the location was used to find the field in which the historic relevé had been made. I was able to locate plots with an accuracy of between 10 m and 500 m. For more than 50% of the plots the site specific accuracy was between 30 m and 50 m in radius. Plots that could not be placed this accurately were situated in level country where the historical references could give better precision to allow for a more accurate localisation than the fieldname alone.

Vegetation relevés

To answer my first question (How did the arable flora change in Switzerland over the last 90 years?) I conducted a re-survey study. From the 4500 relevés made by the mentioned authors between 1927 and 1980, I selected historical plot relevés of wheat, barley, beet or potato fields. Other crops were disregarded as they were only rarely present in the historical surveys. I assigned these datasets to a biogeographic region and further assessed whether the historical relevés contained species that are now red-listed in Switzerland (Moser *et al.*, 2002). Subsequently, I took a stratified random sample of the whole dataset. The strata consisted of biogeographic region, historical author, Red List status and crop type. I selected 700 locations with historical relevés of which I re-surveyed 515 in 2011 and 2012. I only repeated historical relevés if I found the same crop type as in the historical relevés inside the site-specific accuracy-radius. I considered one historical and one contemporary plot per field. An additional 110 relevés were recorded in those regions of Switzerland where no historical data was recorded. This made it possible to complete the present dataset for the whole country. Based on this dataset, regions with a high diversity of arable species could be detected.

Phylogeny

To answer the second question (How did the phylogenetic structure in arable and meadow communities in Switzerland change from historic to contemporary relevés?) I performed an analysis on the phylogenetic structure of meadow and arable communities. Additionally to the re-surveyed arable plots, 232 relevés from historic and contemporary meadows, respectively were selected from the Agroscope database. To analyse the phylogenetic structure of those four communities (historic and contemporary arable and meadow communities) I constructed a supertree for arable and meadow communities, using the pooled taxa of the relevés made in those habitats. The phylogenetic trees were assembled using the online tool “Phylomatic” (Webb & Donoghue, 2005). The structure of the data was analysed with Phylocom using the constructed supertrees and sample data of the

vegetation relevés (Webb *et al.*, 2008). I compared the samples using the net relatedness index (NRI) and nearest taxon index (NTI) compiled by Phylocom.

Soil samples

To answer the third question (Would it be possible to re-establish populations of threatened arable species on abandoned arable fields in the Swiss Alps?) I recorded a seedbank study on former arable fields in Alpine valleys of Ticino and Grisons. At 38 locations, soil samples were taken at the end of September after the last grass was cut, so as not to destroy the harvest. Each site was divided in a field-centre and a field-border zone. The border zone consisted of the outermost 3m of the field. In each zone 21 soil cores with a diameter of 2.5 cm were taken to a depth of 20 cm and then pooled (Dessaint *et al.*, 1996; Smutný & Křen, 2003). I determined the viable seeds in the soil cores by the seedling emergence method according to ter Heerdt (Ball & Miller, 1989; Ter Heerdt *et al.*, 1996). Seedlings were identified based on Hanf (1999) and removed once a week. Plants that could not be identified were planted into a separate pot and grown until they could be identified. Grasses and sedges were only distinguished to the family level.

Results and Discussion

In Switzerland the average species number per plot decreased significantly from historical to contemporary plots by 66% from 22.7 to 7.9 species (n=232, Wilcoxon: $p_{two\text{-}tailed} < 0.001$). The 110 additional relevés had an average species number per field (7.6 species) in the same range as in the re-surveyed ones. If species of the field border were included the average species number per field increased to about 20. This is still significantly lower than in historic fields. It was more likely to find threatened species in the field border than in the plot in the centre of the field. In the field centre, seven of the 15 historically most frequent species were still in the "Top 15" list and all of them were in the "Top 30" list. However, the frequency of common species was much higher in historical than in contemporary plots. In the contemporary plots only 53 species were present in more than ten plots.

Historically, 107 species occurred in more than ten plots. Most species that were no longer present in contemporary plots already had a frequency less than 5% in historical plots. Mean species frequency between historical and contemporary plots declined by 52% from 7.7% to 3.7%.

This decline in average species number per plot is much more pronounced than the decline of 20% I found in the meta-analysis across Europe. Even if only studies starting before 1980 are considered, the respective decline is much smaller (25%). However, recent studies from Germany and Slovakia show a similar decline as this study from Switzerland with 25% and 8%, respectively, (Májeková *et al.*, 2010; Meyer *et al.*, 2013). So even if the decrease of species number per plot is a general trend across Europe, the magnitude differs dramatically among the countries. The meta-analysis yielded no hint at what could have caused these differences as no tested variable (crop type, study design, geographic location, precipitation) showed an influence on the magnitude of the decline in average species number per plot. In Switzerland, the decrease in average species number per plot was not the same across the different biogeographic regions. In regions with many marginally profitable areas, the species decline was not as pronounced as in the intensively farmed regions of the lowlands. Hence, the differences among regions in the meta-analysis could also be due to differences in magnitude of the agricultural intensification in the respective regions. However, I did not have the information needed to test this.

Only few studies from Switzerland for other habitats than arable fields exist to which the above results could be compared. For mountain hay-meadows, no change in total species number was detected in several studies (Fischer & Stöcklin, 1997; Homburger & Hofer, 2012). These studies only covered changes since 1960, but the biggest losses may have happened before 1960 and were thus not detected (Walter *et al.*, 2010). During the last ten years, species richness did not change in any of the recorded habitats of Switzerland according to the Swiss biodiversity monitoring program (BDM, 2013). Still, even if species number did not change, the composition of the plant communities could

still have changed. Many studies as well as found that characteristic species for the respective habitats declined or vanished and were replaced by new and often generalist species (Fischer & Stöcklin, 1997; Stehlik *et al.*, 2007; Peter *et al.*, 2008; Bergamini *et al.*, 2009; Homburger & Hofer, 2012). In Germany, habitats in urban landscapes even showed an increase in total species number due to newly occurring species (Knapp *et al.*, 2010). The average species number in grassland plots of Central Europe declined by 30-50% from 1950 to 2009 (Wesche *et al.*, 2012). While another study found an increase of 30% from 1930 to 2000 (Newton *et al.*, 2012). In accordance to the studies in Switzerland, many studies found a decrease in specialist species and an increase in generalist species (MacDonald *et al.*, 2000; Newton *et al.*, 2012; Wesche *et al.*, 2012). Hence, while average species number increased in other habitats it declined dramatically in arable fields. Which might be due to a more intense use of herbicides in this habitat.

Comparing historical and contemporary plots, plants characteristic of fertilized meadows increased at the expense of species characteristic for arable fields. The total number of traditional arable weed species decreased from 116 to 90. This is in line with studies from grassland systems (Fischer & Stöcklin, 1997; Stehlik *et al.*, 2007; Peter *et al.*, 2008; Bergamini *et al.*, 2009; Homburger & Hofer, 2012). Neophytes, monocotyledons, nitrophileous, wind dispersed, or early flowering species and species with a broad geographic distribution increased. The percentage of shade-tolerant species per plot declined while that of light-demanding species increased. However, the percentage of light-demanding species in the total data set declined. Most herbicides in cereal crops are broadleaf-selective as they were designed to not affect cereals (Fryer & Chancellor, 1970; Wrucke & Arnold, 1985). Hence, grass weeds are not antagonised which could explain the increase in monocotyledons. Compared to traditional agricultural landscapes there are almost no hedges or small woodlands left between the fields (Antrop, 2004). This could explain the decline in number of shade-tolerant species as they can no longer invade fields from such wood-lots. On the other hand are most weed species

characteristic of traditionally managed arable fields light-demanding species and those traditional species declined too or even disappeared. The traditional species are mainly replaced by newly occurring species that are light-demanding as well, such as *Amaranthus retroflexus* L. or *Galinsoga ciliata* Blake. (Landolt *et al.*, 2010). This could explain why the amount of light-demanding species did not change while shade-tolerant species decreased in numbers. The increase in neophytes and species with a broad geographic distribution is probably based in the general increase of intercontinental trade and the introduction of new crop species that brought along their associated weeds. The increase in wind dispersed species could also be explained by the loss of hedges in the agricultural landscapes. As these barriers do not exist anymore, the seeds of wind-dispersed species can be spread wider across the fields (José-Maria *et al.*, 2011). While the increase of nitrophileous species is probably based on higher nutrient levels in the soil due to fertilization, the increase in early flowering species might be due to the change of the sowing season of the crop. As most cereals are nowadays sown in late autumn the crop plants are already fairly high in spring. Therefore, weed species that flower early, get more light until their seeds are ripe than weeds that flower later in the year (Hald, 1999).

In the last century the total species number as well as the richness in families declined between 20% and 25% for both arable and meadow communities across Switzerland. In contemporary arable fields NTI values showed a higher phylogenetic clustering than in historic ones while there is no difference in NRI values. In contemporary meadows, on the other hand NTI and NRI values showed a higher phylogenetic clustering than in historic meadows. Overall, the whole arable communities were more phylogenetically clustered than meadow communities. With increasing phylogenetic clustering I found a decrease in trait diversity for both meadow and arable communities. The trait profile in arable communities, but not in meadows, changed from historic to contemporary arable communities.

After detecting the species loss in agricultural communities, the question arose what causes those losses. Based on the increased phylogenetic clustering from historic to contemporary communities and from meadows to arable fields I assume that this might be due to the effect of the increased environmental filtering (Webb, 2000a; Kraft *et al.*, 2007). As already mentioned, filtering is the result of environmental variables that act strongly selective in a certain habitat. Therefore, only species with the necessary adaptations are able to survive. These adaptations usually evolve only in a few cases. Hence, species with the same adaptation tend to have inherited them from a common ancestor, and are therefore phylogenetically closely related. This would be in line with studies from various habitat-types that found filtering as the main cause for phylogenetic clustering (Graham *et al.*, 2009; Kraft & Ackerly, 2010; Whitfeld *et al.*, 2012).

The shorter the plants in a community flower, the more phylogenetically clustered (NRI) the respective community was. NTI was positively correlated with the percentage of short flowering plants Accordingly, r-strategists had higher percentages in phylogenetically clustered communities, the c- and s-strategists reached higher percentages in less clustered communities. This is in line with the theory of Grime (1977) that disturbance acts as a filter on communities that favours ruderal species. Grime (1977) distinguished three strategy types in species r-, c- and s-strategists. While s-strategists (stress-tolerant) are adapted to scarce resources and extreme environmental conditions, c-strategists (competitive) prefer an environment with abundant resources and rare disturbances. R-strategists (ruderal) on the other hand grow where disturbance levels are high, resources abundant but environmental conditions not extreme. The mean indicator value for nutrients increased from historic to contemporary relevés and with the amount of phylogenetic clustering for contemporary relevés of arable and meadow communities, respectively. As already mentioned, this is probably due to higher nutrient level trough the high input of industrial fertilizer (Robinson & Sutherland, 2002). NTI was negatively correlated with the percentage of herbs and legumes per relevé. Thus, the grasses

monocotyledons increase with phylogenetic clustering. As mentioned above this is likely due to the increasing use of broad-leave specific herbicides(Fryer & Chancellor, 1970). Hence, the main changes in traits can be ascribed to the three main filtering effects of agricultural intensification: fertilizer, herbicides and mechanisation.

In Germany and Slovakia, the loss of species in arable communities were similar to the one I found in Switzerland (Májeková *et al.*, 2010; Meyer *et al.*, 2013). These results suggest that similar processes of environmental filtering might be at work across Europe. If those filtering effects are the same across Europe which has an intensive and highly mechanised agriculture, this might be true for other developed countries as well. It is therefore not surprising, that as studies from Japan and the USA report similar losses of species in arable weed communities (Webster & Coble, 1997; Conn *et al.*, 2011; Yamada *et al.*, 2011). Hence, Switzerland could serve as a model country of what is happening in arable weed communities in countries with modern agriculture. On the other hand, the changes that happened in Switzerland might give a hint at what could happen in developing countries. Up to now it is not clear, which consequences the introduction of modern agricultural practices to those countries will have. Probably, the worrying tendency of decreasing species and family diversity will spread to those countries too if the same measures of intensification are taken. It would therefore be advantageous if agri-environmental measures would be introduced alongside the modern agricultural practices. This is important, as communities in which plant species get lost through environmental filtering, become more phylogenetic clustered (Kraft *et al.*, 2007). Additionally, if these filters change over time the trait diversity and distribution will change with them. The losses of species and traits however, threaten the supply of ecosystem services (Altieri, 1999; Díaz *et al.*, 2007; Isaacs *et al.*, 2008; Díaz *et al.*, 2013).

To ensure that the agricultural land can supply those crucial ecosystem services, it is t important to promote the conservation of arable weeds (Gerowitt *et al.*, 2003). As already mentioned, one way

to do this is the promotion of agri-environmental schemes like wildflower strips or set-aside land. Those measure do help to promote the arable flora (Kleijn & Sutherland, 2003; Kleijn *et al.*, 2006; Eggenschwiler *et al.*, 2010).However, up to now, agri-environmental schemes for arable land are not used as much as would be necessary (Guntern *et al.*, 2013). Likely, this is because they increase the workload and the subsidies paid are not high enough to outweigh that (Eggenschwiler *et al.*, 2010). Therefore, it would be important to improve those schemes so that farmers are more willing to implement them on their land. Another possibility would be, to set up conservation fields in regions that still have a high diversity of arable weed species or on fields that once had a rich arable flora. So that abandoned fields that are ploughed again can sport a high diversity of arable species, the seeds of those must still be present in the seedbank.

Out of about 3500 seedlings, 119 plant species were identified but only 49 species were typical arable weeds. Only one of those is red listed in Switzerland (Moser *et al.*, 2002). With the method I used between 81 and 100% of the viable seeds germinate (Ter Heerdt *et al.*, 1996). Therefore, it is quite likely that I did not miss rare species with viable seeds in the soil sample. Additionally, most seeds have a patchy distribution and therefore the soil cores were randomly distributed on the sub sites on approximately the same area (Dessaint *et al.*, 1991). Hence, rare species could only go unnoticed if the number of soil-cores taken was too small. As the number of samples was relatively big for the small fields I sampled, this should not be the case. I found a significant negative influence of the combination of altitude and slope on the total number of arable species as well as on the percentage of re-found species that germinated. Whether the sample was taken in the border of the field or in the field centre had no influence on the number of arable species that germinated. Therefore, even if the field borders usually have a higher species diversity (Kleijn & Verbeek, 2000), this is not represented in the seedbank after some decades. Probably, the loss of viable seeds is exponential which would lead to similar numbers of viable seeds after a long time. The seed

longevity of the arable weeds that germinated was mostly between 20 to 100 years, but also four species with seed longevity of over 100 years. I found no arable weeds among the seedlings with seed longevity shorter than 20 years. This is not surprising as the fields were conversed to grassland over 30 years ago. However, also species that were not re-found had a high seed longevity and could, even if they were not detected in this study, germinate if the field would be ploughed again. Hence, the surveyed meadows had a small potential to promote threatened arable weeds if tilled again. To the same conclusion comes a seedbank analysis on former arable land that was turned to meadows of two students in the Engiadina Bassa (Battaglia & Hodler, 2008). In soil samples of 12 meadows, they found 18 arable weed species of which only one was red listed.

In spite of these results, some successful projects on fields for the conservation of arable weeds are implemented in Switzerland. For example, meadows on former arable fields in Biela and Brentjong (VS) were tilled again and afterwards farmed organically (Staatsrat, 1999). Probably, those parcels were never intensively managed. Hence, the historical species richness and abundance was high and therefore a higher amount of seeds was accumulated in the seedbank (Albrecht, 2005). Additionally, a heterogeneous landscape – as the one in Brentjong - increases the chance for a successful conservation project as nearby ruderal habitats serve as a source for arable weed (Aavik & Liira, 2009). The chances for the recolonization of rare species are very low if there are no populations nearby from where those species could be stocked up(Bischoff & Mahn, 2000; Bischoff, 2005). To bring those rare species back, it might be necessary to use appropriate seed-mixtures. This approach is already used successfully in Germany in a project called “100 fields for diversity” (Meyer *et al.*, 2008). Nevertheless, one has to be aware that seed-mixtures of arable weeds may contain non-adapted non-regional genotypes (Vander Mijnsbrugge *et al.*, 2010). This would decrease the genetic diversity of the respective region if the regional genotype still exists.

I found significant differences in average species number per plot depending on the biogeographic region. In mountainous regions the average species number was higher than in the lowlands. However, the five relevés with the highest species number where from the lowland. Therefore, two approaches for conservation are needed. (1) In the lowland fields with a high diversity of arable weed species need to be detected and the protected. This thesis made a first step to detect such fields. Another effort was made by the "Ressourcenprojekt zur Erhaltung und Förderung gefährdeter Schweizer Ackerbegleitflora" (Agrofutura, 2012). (2) In the mountains, arable farming should whether be intensified nor abandoned.

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Chapter I

75 Years of Change in the Arable Flora of Europe: A Meta-Analysis

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Summary

Changing agricultural practices has dramatically altered the arable flora of Europe over the last 75 years. We made a meta-analysis of the available literature to assess the dynamics of species richness and species traits in the arable flora across Europe during this time period. We found a total of 32 studies, yielding 53 datasets with an average number of 252 plots. Average species number per plot of arable plants across all datasets considered declined by about 20% during the last 75 years. However, twelve of these datasets showed an increase in average species number per plot: including all studies starting after. Plant species preferring nutrient rich sites, neophytes and monocotyledons generally increased since 1980 while characteristic or threatened species of arable weed communities further declined. This temporal development of the European arable flora suggests that conservation measures such as ecological compensation areas like unsprayed field margins or wild-flower strips have helped to slow the decline of the arable flora in terms of species number, but not in terms of characteristic or threatened arable weeds. Hence, more specific measures are necessary to stop this decline, making sure that these measures are advantageous for rare and characteristic arable species but not for harmful weeds.

Keywords: Biodiversity, conservation, decline, functional traits, temporal development, weed

Introduction

Agricultural land covers about 40% of the land area of Europe (Georgieva & Martins, 2012) and is thus one of the biggest biomes in Europe. Humans have been cultivating land since about 5000 years ago, and this has led to a remarkably rich arable flora (Holzner & Immonen, 1982). This flora was assembled from both indigenous and imported species (new crops from transcontinental commerce and migration) from all over the world, albeit mostly from the Middle East and the Mediterranean (Landolt et al., 2010). Generally, the pool of arable species increases from northern Europe to the Mediterranean (e.g. Finland: 120 weed species; Italy: over 450 weed species; Holzner & Immonen, 1982, Lososová et al., 2004).

Since the Second World War, agricultural practices in Europe have changed dramatically. These changes took place in all sectors of agriculture, especially regarding dramatically larger inputs of industrial fertilizer, pesticides and other chemicals (Robinson & Sutherland, 2002, Herzog et al., 2006, Walter et al., 2010). In addition, the timing of sowing has shifted from spring to autumn for many crops, and a variety of new crops have become widespread, while many traditional crops and crop varieties almost disappeared (Andreasen & Streibig, 2010, Bundesamt für Statistik, 2013). As effective seed cleaning processes have been implemented, seeds of arable weeds are no longer spread onto fields via crop seed (Van Elsen, 1994). Agricultural practices have also altered due to changes in political settings, e.g. in many countries of Eastern Europe (Bouma et al., 1998, Májeková et al., 2010), where farmers now have greater flexibility than they had before: during the last decades, field sizes increased hand in hand with a general structural impoverishment of arable landscapes (Kienast, 1993). As a consequence of all these changes, many characteristic arable weed species adapted to traditional, less mechanized and more small-scale agricultural systems have become rare and are now red-listed in various European countries: up to 77% of the arable flora is threatened in certain countries, and across all European countries, a total of 582 species are threatened (Albrecht & Bachthaler, 1990, Andreasen et al., 1996, Moser et al., 2002, Storkey et al.,

2012). Weeds adapted to modern field management optimized for higher crop yields – such as species tolerating higher nutrition levels, less acidic soils and higher herbicide input – increased substantially in abundance and distribution (Kutzelnigg, 1984). In contrast, traditional arable weeds are short, late-flowering, possess large seeds and need high light conditions and low nutrient inputs, making modern agricultural practices unsuitable to them (Booth & Swanton, 2002, Storkey et al., 2010). This is why, in the 1980s, several European countries introduced payments for conservation measures to protect the biodiversity on arable land such as unsprayed field margins in Germany or Great Britain (Kleijn & Sutherland, 2003). In addition, ecological compensation areas (e.g. wild-flower strips) and organic or integrated farming were financially promoted, for instance in Switzerland (Art. 18 NHG, Art. 18 NHV). Up to now, few studies assessed the influence of such agri-environmental measures on the biodiversity of arable fields (Concepción et al., 2008, Eggenschwiler et al., 2010, Kleijn et al., 2011, Meyer, 2013).

Surveying the flora of arable fields has a long tradition in Europe, starting at the end of the 19th century. The first investigations into changes in the flora of arable fields due to changes in agricultural practice were published in the 1960s (Bachthaler, 1968), with many publications appearing in the 1980s. It is still a popular research area (Storkey et al., 2012). Most of these studies were restricted to a single region or country, and no formal European-wide review of changes in the arable flora has been conducted yet. We therefore undertook a meta-analysis in order to comprehensively assess how the arable weed flora changed across Europe during the last 100 years. We concentrated on changes in the number of species per plot and tested the following three hypotheses. (1) Over the last 100 years, the number of arable plant species per plot declined all over Europe. (2) Since the 1980s, numbers of arable species per plot ceased to decline or even increased due to the implementation of agri-environmental measures and a trend towards low-input farming. (3) There spectrum of weed-specific functional traits has changed during the last century.

Meta-analyses are a useful tool to summarise results across different studies, but they also have some disadvantages (Gurevitch & Hedges, 1999). Firstly, meta-analyses are only as good as the data on which they based. Studies without significant results are seldom published and thus introduce publication bias into meta-analysis (Borenstein et al., 2009). Moreover, various biogeographic regions, varying plot sizes, different survey methods and poor data reporting are common in published articles, and ecological studies are hardly ever replicated in a strict statistical way (Gurevitch & Chester, 1986). Despite these difficulties, meta-analyses have the potential to be more informative about general trends than single studies or traditional reviews.

Methods

Data set on species number per plot.

We compiled studies from the literature on the number of weed species per study plot at two or more points in time. We considered articles published before December 2012 in ScienceDirect, Web of Knowledge, JStor and Google Scholar using the following search terms: chang* AND weed* AND ('arable' OR 'seget*'), ('change*' AND 'weed*') AND ('arable' AND 'segetal*') AND communit*. We also consulted the reference lists of the detected articles Additionally, we used Google to search for articles in German or French language. We further considered those articles if they contained the above mentioned terms (or their equivalents in German and French) in the titles. Grey literature, such as governmental reports or Master-theses, were included if they could be obtained

Articles were considered if the following criteria were met: (1) the study site was in Europe, (2) reported data for average species number per plot (in the text, tables or figures), (3) the study was not designed to show differences between farming systems, and (4) the time period between consecutive surveys was at least five years. Experimental studies were not included. We found a total of 32 relevant studies. Several studies reported results for more than one crop type and/or more than two points in time. In these cases, all comparisons between two points in time were included in the analysis as independent entries in the dataset. This resulted in 53 entries in the whole dataset.

An additional 30 studies might have met the above criteria but it was impossible to access them (old and grey literature). The 32 studies covered the time period from 1939 to 2011. Mean number of plots per data entry was 252, the whole dataset contained a total of over 10'000 relevés.

We extracted further information from these 32 studies, namely crop type, plot area and size of study region. We included crop type in the analysis, because root crops usually have a lower number of associated weed species than cereals (Delarze & Gonseth, 2008). Plot area was tested, because small plot sizes do likely not reflect long-term changes in the weed flora but simply reflect small-scale variation in species number, even within the same field (plot area varied substantially from 0.1 to 4000m^2). The size of study region was included, as a large study regions probably contain subregions with different temporal developments of the arable weed flora and as sampling densities are often higher in smaller than in larger study regions, leading to a better estimate of average species numbers in smaller study regions.

In addition, we took longitude and latitude as well as precipitation of study regions into account. The species pool of arable species decreases from the Mediterranean to Northern Europe (Holzner & Immonen, 1982, Lososová et al., 2004). We therefore wanted to test whether latitude and longitude have an influence on average species number per plot. We also included precipitation as environmental factor as the amount of rain often changes drastically among biogeographical regions. Annual precipitation of study regions was taken from existing data bases (http://www.klimadiagramme.de/). All extracted information from the 32 relevant studies is given in Table 1. However, we used a response ratio (see below) thus avoiding issues of species area curves or species pools as the compared data from within the same region always had the same plot sizes (Hedges et al., 1999).

Analysis of change in species number

The response ratios for the meta-analysis and other statistics were calculated with METAWIN (Rosenberg et al., 2007) and the packages "metafor" (Viechtbauer, 2010) and "bootES" in R (Gerlanc

& Kirby, 2013). In usual meta-analyses, an effect size and a variance for each study are needed and out of these values, a weighted mean of effect sizes is computed, with more precise effect sizes having a higher weight. The variance of an effect size is based on the standard deviation given in a given study. As standard deviations (or similar measurements of variation) around the average species number per plot were only available for a small number of the 32 studies considered in the present study, we used the response ratio as an effect size, which can also be calculated without knowing standard deviations. The response ratio is defined as the ratio of the means of species number per plot between historical and recent studies (Borenstein et al., 2009). Bootstrapping was used to calculate 95% confidence intervals. If the confidence interval overlapped with zero, the effect size was considered to be non-significant. Using a response ratio has the additional benefit that it avoids issues of different plot areas (Hedges et al., 1999). We calculated the response ratio for different datasets: (1) for the whole dataset (2) for datasets grouped by crop type (cereal, root crop or undefined) and (3) study design. The variable design was split into two groups, namely random and repeated study designs. In the first group, plots had been randomly distributed over a study region and were not paired in time (N = 21 data entries). In the second group, plots had been repeated at the same location at two points in time (N = 32 data entries). Random studies with an only small number of plots are less accurate in estimating the change in average species number than repeated studies (Borenstein et al., 2009). Additionally, we built general linear models (GLM). The estimation of means gets more precise with increasing sampling effort, therefore we used the ratio of the number of samples per area of the study region as a weighting factor in GLMs.

In order to analyse the effect of temporal changes on the number of arable species, we split the 32 studies into the following three groups: (1) studies ending before or by 1980, (2) studies beginning before and ending after 1980 and (3) studies beginning in or after 1980. We choose 1980 as threshold, because from 1980 onwards less intensive agricultural management such as decreasing

use of herbicides or more extensive farming started in many European countries (ECC Regulation 797/85, 1985, Kleijn & Sutherland, 2003).

Meta-analysis of data without standard deviations is less precise than an analysis of data with standard deviations. Therefore, we additionally analysed those 24 entries in our dataset that provided standard deviations (Table 1) to verify the results that we received from the analysis of the whole dataset. We calculated an average response ratio weighted by the variance of the effect size, so that data with smaller variance had a higher weight in the analysis. We then assessed the homogeneity of this effect sizes across studies according to the standard procedure of meta-analysis (Gurevitch & Hedges, 1999, Borenstein et al., 2009). We included the same factors into mixed effects models in R as we used for the whole dataset; namely latitude and longitude, crop-type, study design precipitation and time period (Viechtbauer, 2010).

Publication bias

To check for publication bias, we used the Rosenberg fail-safe N (Rosenberg, 2005) and the funnel plot. The fail-safe N represents the number of studies without a significant result which had to be included in the analysis in order to change the outcome of the analysis. A funnel plot is a scatterplot of standard errors against effect sizes. If studies are not symmetrically distributed then there is publication bias (Borenstein et al., 2009).

Data on functional traits

Out of the 32 studies, only 20 reported on plant functional traits. Traits that were mentioned more than once were noted. Additionally to reproductive and life-strategy traits, we also included information on “indicator species”. Indicator species are characteristic of traditional arable weed communities (e.g. Delarze & Gonseth, 2008). As the number of studies reporting on plant functional traits was small and diverse, we did not subject them to a statistical analysis and only analysed the data in a descriptive way.

Results

The studies were not equally distributed across Europe. Few data were from Mediterranean areas (Fig. 1), where arable fields had the richest initial arable weed flora (Shmida & Wilson, 1985). Additionally, we did not find data for some northern countries. More than one third of all studies were conducted in Germany, and the majority of studies overlapping with the year 1980 were from the Czech Republic.

Analysis of the whole dataset

The meta analysis showed that the mean effect size per data entry varied between -1.099 and 0.605. The overall mean effect size (log response ratio) was lnRR = -0.208 (95% confidence interval CI: -0.1126, -0.3070). Hence, the average species number of arable weeds per plot declined by about 20% from an overall mean of 33.5 to an overall mean of 27.5, rejecting our null-hypothesis of no change. In 13 data entries average species number per plot increased, while it decreased in 40 data entries. Analysing temporal subgroups, we found a significant decline in average species number for studies conducted before 1980 (lnRR =-0.242; CI:-0.356, -0.122) and for those studies beginning before and ending after 1980 (lnRR =-0.245; CI:-0.409, -0.077). For studies beginning after 1980, however, we found a tendency for increasing species number with lnRR = 0.133, but this trend was not significant (CI:- -0.092, 0.357). There was no influence of study design or crop type on mean effect size (Table 2, first column).

In GLMs, crop type, study design, geographic latitude and precipitation showed no significant effects on average species number per plot (Table 3). We found a significantly negative influence on the mean effect size of studies ending before 1980 and overlapping 1980. Longitude also had a significantly positive effect on mean effect size, indicating that average species number per plot declined less in eastern than in western countries (Table 3).

Analysis of dataset with standard deviations

In the meta-analysis, the weighted mean effect size of the datasets with standard deviations was lnRR= -0.126 (CI: -0.249 -0.002, z = -1.988, p=0.047; Fig. 2). This translates into a decrease in average species number per plot of about 13% across time. Heterogeneity between studies was significant (Q_{tot}: 3299.3, df=23, p<0.001, I2=99.3), indicating that most of the observed variance was real. We found no significant change in mean effect size regarding study design or crop type (Table 2). However, there was a significant increase in mean effect size from the group "before 1980" to the group "after 1980" (Fig. 2). So, while average species number per plot decreased in studies ending before 1980 it increased in studies beginning after 1980.

In the mixed effect models, neither precipitation, longitude, latitude, area of study region crop type nor time period had a significant effect on change in average species number per plot (Table 4).

Publication bias

We found no evidence for publication bias. The funnel plot was symmetric and 6.3×10^{13} studies without significant results would have been needed to change the outcome of the results

Trends in functional traits

Eleven functional traits were not associated with arable weeds that changed (either positively or negatively) in frequency over our study period. Three traits are lined to species that have increased in frequency, and eight traits are associated with species that have become more rare.

Species that lost importance either belonged to traditional arable weed communities (e.g. *Adonis aestivalis* L. or *Agrostemma githago* L.) or were species growing under extreme pH-conditions (e.g. *Myosurus minimus* L. or *Scleranthus annuus* L.). These arable weeds are currently rare and threatened. Species that became more common prefer nutrient-rich sites (e.g. *Polygonum lapathifolium* L.), were monocotyledons or herbicide-resistant (e.g. *Alopecurus myosuroides* Huds.), wind-dispersed (e.g. *Aphanes arvensis* L.) or neophytes (e.g. *Nicandra physalodes* (L.) Gaertn.). Only

in Slovakia and the Czech Republic did some characteristic indicator species of traditional arable communties increase in numbers (e.g. Lathyrus tuberosus L., Silene noctiflora L.; Kropàc, 1984, Májeková et al., 2010).

Discussion

In this study, we showed that the average number of arable weeds per plot generally declined by about 20% across Europe during the last 100 years. This result is in line with other studies from different ecosystems all over the world reporting on species decline. For instance, a recent study found that the number of plant species in mountain meadows also declined by about 20% during the last 70 years (Homburger & Hofer, 2012). Similarly, Stehlik et al. (2007) found a plant species loss of 28% across habitat types in a local flora. However, the species decline in agricultural land used land in Europe of 23% (de Heer et al., 2005) is still lower than the 30% decrease observed across all ecosystems worldwide (Butchart et al., 2010).

Decline of arable weeds per plot during the last 75 years

In accordance with our first hypothesis, the average number of arable species per plot declined by about 20% (13% if calculated from the dataset with standard deviation). In contrast, a review by Albrecht and Bachthaler (1990) from Germany found a much larger decrease in weed species of about 50% between 1930s and 1980. This discrepancy was probably due to the influence of studies from the Czech Republic in our study: in the Czech Republic, the decline in arable weeds was not as pronounced as in other countries (Kropàc, 1984, 1988). The change to more intensive agriculture in the Czech Republic took place after 1980 (Májeková et al., 2010). Therefore, a more pronounced decrease in average species number per plot in the Czech Republic would be expected after this time. In fact, a study conducted later on in this region did show a higher decline in average species number per plot (Tyser et al., 2009). Such regional differences between western and eastern European countries are reflected by the significant effect of longitude on effect size that we detected in our study (Table 2). However, as we did find no influences of latitude, precipitation, different study

design nor crop-type on the change in average weed species number per plot, the observed decline is a general trend across Europe, with only slight differences among regions or countries, probably due to general changes in agricultural practice (Stoate et al., 2001). Unfortunately, information about tillage or other explicit farming practices were rarely available from the studies included in our analysis, and we can therefore not test for explicit changes in agricultural practices.

Does the number of arable weeds increase again due to agri-environmental measures?

The implementation of agri-environmental schemes increased across Europe from 1980 onwards. Before 1980, hardly any agri-environmental schemes were implemented. We thus chose this year as a threshold in the present analysis. In fact, in our meta-analysis, the studies providing some measurement of variance and beginning after 1980 showed a significant increase in average species number. Similarly, the whole dataset showed the same trend for increasing average species numbers of arable weeds, but it was statistically not significant. For instance, an increase in the average number of arable weeds per plot was reported in recent studies (e.g. Andreasen & Stryhn, 2012). These results were thus in line with our second hypothesis. It seems that the measures taken to preserve biodiversity on agricultural land since the 1980's, such as organic farming, ecological compensation areas, unsprayed field margins or wild-flower strips (Kleijn et al., 2011), were effective, at least in terms of species numbers. While it is impossible to confirm agri-environmental schemes to be the factor causing this increase in species number from our dataset, our results are congruent with other studies inferring a positive effect of agri-environmental measures on species richness (Kleijn & Sutherland, 2003, Bengtsson et al., 2005, Aviron et al., 2008). However, another study considering complete farmland biodiversity detected only few studies supporting such a claim (Kleijn et al., 2011). One reason for this contrasting judgment on the effectiveness of agri-environmental schemes might be that species numbers do not reflect the occurrence of characteristic or endangered species per se. However, changes in the frequency of these less common species are difficult to detect (Andreasen & Stryhn, 2008), but it is mostly these species that we are interested in

for conservation. In fact, regarding arable weeds, sowing seeds of rare and characteristic arable weeds such as *Consolida regalis* Gray or *Nigella arvensis* L. locally increased weed diversity (Meyer et al., 2008, Kohler et al., 2011).

Plant functional traits

Functional traits can help to give information on the ecological services arable weeds may provide. Desirable weeds would ideally be threatened species, adapted to low input of nutrients and produce a lot pollen, nectar or seed. Such species would not only maintain high plant diversity but also nourish birds and beneficial organisms such as bees and green lacewings. These beneficial organisms would in turn help to maintain high yields of insect-pollinated crops and thus lower the necessary input of chemical pest controls (Isaacs et al., 2008).

Unfortunately, most studies in our dataset lacked a commented species list and only few directly reported on changes in plant functional traits. We can thus only speculate on the third hypothesis posed in this study, i.e. the nature of the species that increased since 1980 and thus led to a trend of increasing average weed species. Are these increasing species really the nowadays rare weeds characteristic for traditional arable farming such as *Adonis* sp. or *Legousia* sp. or are these rather common species that are widely distributed or even problematic invasives?

Table 5 reporting on our limited dataset suggests that increasing arable weeds are linked with traits such as high nutrient demand, herbicide resistance or neophyte status. This indicates that it was rather the weeds problematic for agriculture which increased in number and not the rare, threatened, traditional arable weeds which usually have a short height, large seeds and are late-flowering plants (Storkey et al., 2010). This finding is not surprising given that arable lands nowadays face high nutrient and herbicide inputs (Robinson & Sutherland, 2002); an agricultural practice that seems to favour problematic weeds. However, our study suggests that also wind dispersed species such as *Aphanes arvensis* L. or grasses were favoured. Potentially, this could be due to modern agricultural landscapes being less structured by trees, hedgerows or ruderal sites than in former

times. In modern landscapes, there should thus be fewer barriers to wind dispersal (José-Maria et al., 2011). However, for most functional traits, neither did we detect a clear pattern nor did the studies we reviewed.

Limitations of our dataset

The analyses we are presenting in the present study suffer from several shortcomings.

(1) For the whole dataset, we only dealt with relative changes in the number of arable weeds per plot as it is not possible to perform meta-analyses based on means without standard deviations (Hedges et al., 1999). Additionally, total species number should not be directly compared, because of different sizes of the available species pools in different regions (Holzner & Immonen, 1982). While more information on the actual species level in the different countries might allow precise statements on the situation of arable weeds. However, this study gives valuable insight in the general expanse and direction of change in arable weed communities.

(2) As mentioned above and in line with other studies (Bengtsson et al., 2005, Kleijn et al., 2006, Marshall et al., 2006) we found a trend to increasing numbers of weed species per plot in more recent studies. One could also argue that at some low level (the valley floor, so to say), species number will not drop anymore and that subsequent increases are to be expected because of an increasing abundance of species problematic to agriculture. However, the two studies in our dataset that studied change in arable weeds after 1980 (Andreasen & Stryhn, 2008, Andreasen & Stryhn, 2012) not only found an increase in average species number per plot but they also found more species in the total species pool, more species gained than lost and a higher amount of species increasing in frequency than decreasing in frequency. It would therefore be valuable to repeat studies that were conducted in the 80s (e.g. Bachthaler, 1985, Braun, 1988, Kropàc, 1988, Trzcinska-Tacik, 1991) to see if the trend for increasing numbers of weed species could be confirmed.

(3) Most studies in our dataset were conducted in Germany and the Czech Republic: most of studies thus originated in Central Europe. This could be a reason why we found no influence of latitude on the number of weed species (Tables 3, 4) in the analysis of the whole dataset. However, even in the dataset with standard deviations we found no influence of geographic location. We thus believe that there was no problem with the geographic distribution of studies in our dataset (e.g. a lack of data in South-Eastern Europe) or that the longitudinal difference we detected (Table 2) reflect ecologically meaningful differences among European regions (see above).

(4) Publication bias could lead to wrong conclusions in meta-analyses. However, we found no evidence for publication bias in the present study and can thus safely exclude this source of error.

Conclusions and implications

The average number of arable species per plot have clearly declined during the last 75 years, potentially due to modern agricultural practices causing high fertilizer and herbicide input and introducing more intensive farming. Nevertheless, increases in average species number per plot after 1980s suggest that measures taken to conserve biodiversity in agricultural landscapes and arable fields also had a positive influence on the richness of arable weeds. However, it looks like nutrient-loving rather wide-spread weeds mostly profited from these measures. In fact most rare species will not spontaneously return to formerly intensively-used agricultural landscapes because regional or local species pools are now depauperate. As we could not investigate the influence of functional traits on losses and gains in arable weeds in a statistical framework, their effects still rests to be determined. Without such functional information, however, it is difficult to disentangle the processes behind species decline, although such knowledge would be essential in order to preserve biodiversity on arable land.

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Figures

Fig. 1: Map showing the number of data entries in the whole dataset on changes in arable weeds per European country (ending before 1980/overlapping with 1980/beginning after 1980).

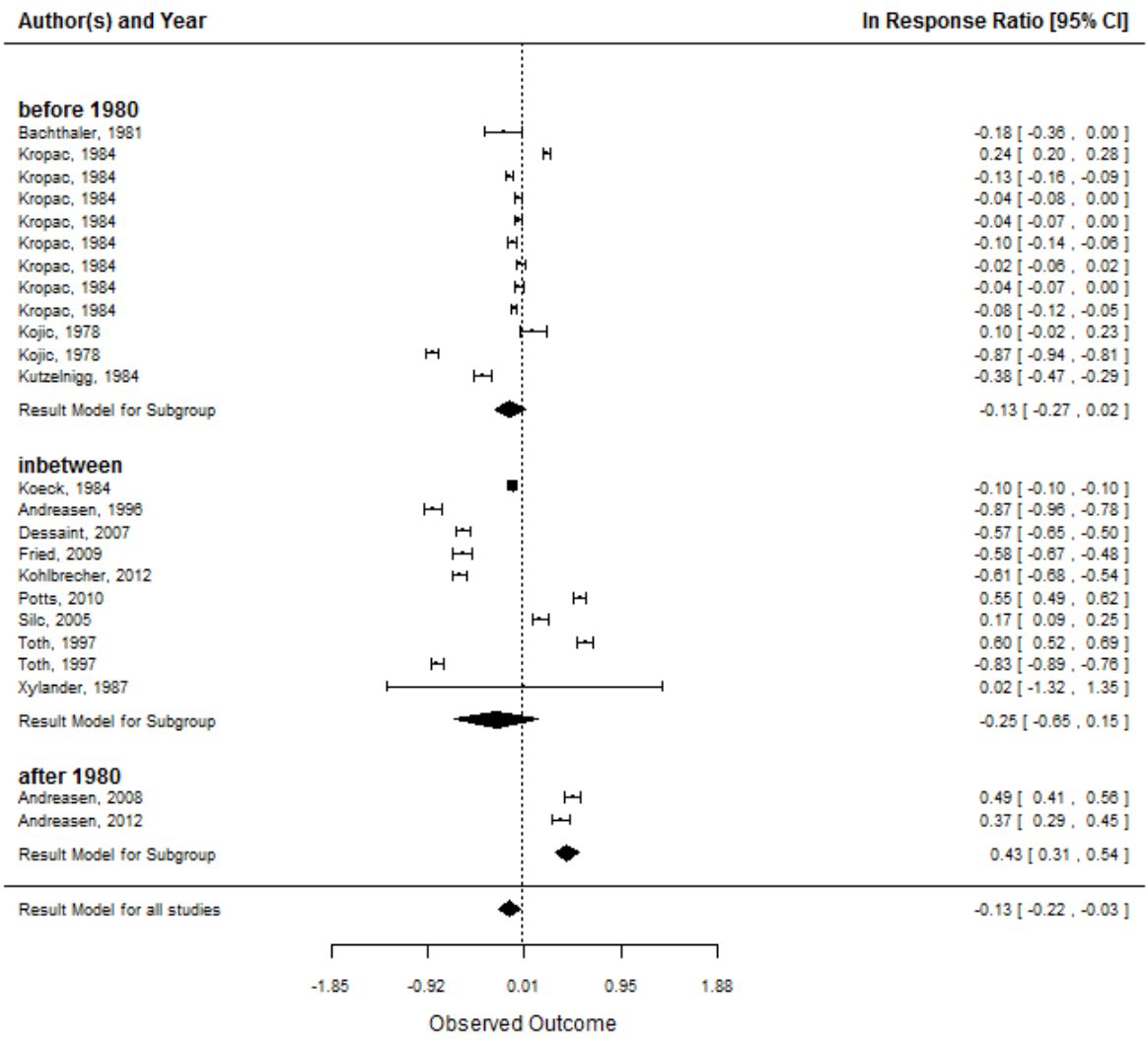

Fig. 2: Mean effect sizes (log response ratio of the average species number per plot; squares) of the 24 data entries in the data set with standard deviation (bars) and the respective grand means (diamond) for three time periods (beginning after 1980, ending before 1980, overlapping 1980). Studies with bars crossing the dashed line have a non-significant effect.

Tables

Table 1: Information on studies used for meta-analysis. Design: studies where plots were either repeated at the same location as the historical ones or taken from random plots across a study region. Crop types were split into root crops or cereals. If the two crop types were not distinguished in the respective study, crop type was set as "all". Plot area: size of plots as reported in respective study.

Reference	Start of study	End of study	Country	Annual precipitation [mm/a]	Longitude [°]	Latitude [°]	Design	Crop-type	Area of the study region km2	Number of historical relevés	Number of recent relevés	Plot area [m^2]	Historical average species number	Recent average species number	Standard deviation (or similar measure)	Information about functional traits
Andreasen and Stryhn (2012)	1987	2004	Denmark	600	56	10	random	all	43094	157	167	0.1	3.13	4.53	yes	no
Andreasen et al. (1996)	1967	1989	Denmark	600	56	10	random	cereal	43094	139	213	0.1	6.28	2.63	yes	yes
Andreasen and Stryhn (2008)	1987	2004	Denmark	600	56	10	random	cereal	43094	213	240	0.1	2.63	4.28	yes	yes
Bachthaler (1982)	1950	1980	Germany	789	51	10	random	all	70552	25	32	-	97.4	81.1	yes	yes
Bachthaler (1985)	1948	1965	Germany	789	51	10	random	cereal	70552	653	662	-	26.6	22.3	no	no
Bachthaler (1985)	1948	1980	Germany	789	51	10	random	cereal	70552	-	-	-	26.6	14.1	no	no
Bachthaler (1985)	1948	1965	Germany	789	51	10	random	root	70552	761	650	-	25.6	15	no	no
Bachthaler (1985)	1948	1980	Germany	789	51	10	random	root	70552	-	-	-	25.6	15.4	no	no
Baessler and Klotz (2006)	1959	1979	Germany	789	45	11	random	all	4	120	115	100	20	14	no	no
Baessler and Klotz (2006)	1979	2000	Germany	789	45	11	random	all	4	115	220	100	14	15	no	no
Braun (1988)	1965	1974	Germany	789	49	8	repeated	all	75.3	42	42	-	17.4	12.9	no	no
Braun (1988)	1966	1971	Germany	789	49	12	repeated	all	93.6	37	37	-	16.9	12.7	no	no
Braun (1988)	1971	1980	Germany	789	49	12	repeated	all	93.6	37	37	-	12.7	11.5	no	no
Braun (1988)	1974	1985	Germany	789	49	8	repeated	all	75.3	42	40	-	12.9	11.5	no	no
Bunce et al. (1999)	1978	1990	Britain	850	54	3	random	all	-	124	124	-	6.69	5.08	no	no
Cirujeda et al. (2011)	1976	2007	Spain	300	41	1	random	cereal	-	21	138	2000	9	3	no	yes
Davy (2006)	1978	2002	Britain	850	51	1	repeated	all	2.52	22	22	100	7.6	7.7	no	no
Dessaint et al. (2007)	1968	2006	France	825	47	5	repeated	all	8763	757	315	2000	16.5	9.3	yes	yes
Fried et al. (2009)	1970	2000	France	825	51	1	repeated	all	6000	158	158	2000	16.5	9.28	yes	yes
Hilbig and Jage (1984)	1970	1980	Germany	789	51	12	random	all	770	-	-	-	-	-	no	yes
Köck (1984)	1967	1979	Germany	789	51	13	random	all	60.67	45	67	-	22.56	20.4	yes	yes
Kohlbrecher et al. (2012)	1960	2011	Germany	789	51	11	repeated	all	1035	-	-	-	24	13	yes	no

Reference	Start of study	End of study	Country	Annual precipitation [mm/a]	Longitude [°]	Latitude [°]	Design	Crop-type	Area of the study region km2	Number of historical relevés	Number of recent relevés	Plot area [m^2]	Historical average species number	Recent average species number	Standard deviation (or similar measure)	Information about functional traits
Kojic (1978)	1952	1977	Serbia	500	44	21	repeated	cereal	-	5	5	-	25.4	10.6	yes	no
Kojic (1978)	1952	1977	Serbia	500	44	21	repeated	root	-	5	5	-	15	16.6	yes	no
Kropàc (1984)	1954	1962	Czechia	450	50	13	repeated	cereal	3	40	40	100	62	57	yes	no
Kropàc (1984)	1962	1972	Czechia	450	50	13	repeated	cereal	3	40	40	100	57	55	yes	no
Kropàc (1988)	1962	1985	Czechia	510	50	15	repeated	cereal	14000	28	28	100	34	28	yes	yes
Kropàc (1988)	1962	1985	Czechia	510	50	15	repeated	cereal	14000	28	28	100	33	25	yes	yes
Kropàc (1988)	1962	1985	Czechia	510	50	15	repeated	cereal	14000	28	28	100	31	26	yes	yes
Kropàc (1988)	1962	1985	Czechia	510	50	15	repeated	cereal	14000	28	28	100	34	27	yes	yes
Kropàc (1988)	1962	1985	Czechia	510	50	15	repeated	cereal	14000	28	28	100	32	30	yes	yes
Kropàc (1984)	1972	1977	Czechia	450	50	13	repeated	cereal	3	40	40	100	55	54	yes	no
Kropàc (1984)	1977	1981	Czechia	450	50	13	repeated	cereal	3	40	40	100	54	49	yes	no
Kropàc (1984)	1954	1962	Czechia	450	50	13	repeated	root	3	40	40	100	55	53	yes	no
Kropàc (1988)	1962	1985	Czechia	510	50	15	repeated	root	14000	30	30	100	31	21	yes	yes
Kropàc (1988)	1962	1985	Czechia	510	50	15	repeated	root	14000	30	30	100	35	33	yes	yes
Kropàc (1984)	1962	1972	Czechia	450	50	13	repeated	root	3	40	40	100	53	51	yes	no
Kropàc (1984)	1972	1977	Czechia	450	50	13	repeated	root	3	40	40	100	51	45	yes	no
Kropàc (1984)	1977	1981	Czechia	450	50	13	repeated	root	3	40	40	100	45	57	yes	no
Kulp and Preuschhof (1985)	1950	1983	Germany	789	53	9	repeated	all	419	190	190	25	18.6	13.5	no	no
Kutzelnigg (1984)	1950	1981	Germany	789	51	7	random	all	200	106	106	500	17.6	12	yes	yes
Maire (1999)	1975	1996	Switzerland	1458	46	8	repeated	all	51.55	15	34	-	21.1	25	no	no
Májeková et al. (2010)	1949	2006	Slovakia	650	48	17	random	all	1000	347	121	100	14.7	17.7	no	yes
Meisel (1979)	1945	1977	Germany	789	52	9	random	all	1	72	50	-	30	10	no	yes
Mittnacht (1980)	1948	1978	Germany	789	48	10	random	cereal	16	-	-	100	21.9	16.2	no	no
Otte (1990)	1951	1986	Germany	789	49	11	repeated	all	357104	6	6	75	33.7	41.4	no	no
Pàl (2004)	1969	2003	Hungary	550	46	18	random	all	-	161	5	50	35	22.5	no	no
Potts et al. (2010)	1968	2005	Britain	850	51	0	repeated	cereal	62	106	106	1	1.03	1.79	yes	no
Šilc and Čarni (2005)	1939	2002	Slovenia	1000	46	15	random	all	50	-	-	-	22	26	yes	no
Toth et al. (1997)	1949	1996	Hungary	550	47	20	random	all	93030	202	202	25	86.4	37.8	yes	no

Reference	Start of study	End of study	Country	Annual precipitation [mm/a]	Longitude [°]	Latitude [°]	Design	Crop-type	Area of the study region km2	Number of historical relevés	Number of recent relevés	Plot area [m^2]	Historical average species number	Recent average species number	Standard deviation (or similar measure)	Information about functional traits
Toth et al. (1997)	1949	1996	Hungary	550	47	20	random	all	93030	202	202	25	37.8	69.2	yes	no
Trzcinska-Tacik (1991)	1947	1988	Poland	662	50	20	repeated	cereal	4000	38	40	-	48.5	39.75	no	no
Tyser et al. (2009)	1975	2005	Czech	510	50	15	repeated	all	52065	7	-	100	32.86	17.71	no	no
Xylander (1987)	1967	1985	Germany	789	51	12	repeated	cereal	150	42	42	100	9.95	10.1	yes	yes

Table 2: Mean response ratio (lnRR; ratio of change in average species number per plot) with 95% confidence interval. Plots were either randomly distributed or repeated at the same location. Crop types were either cereals, root-crops or undefined (all crops). Studies were beginning after 1980, ending before 1980 or overlapping the year 1980. The last row shows the results of the null model without additional factors (i.e. whole dataset included). Significant changes are marked with an asterisks.

	Whole dataset analysed with R using bootstrap	Dataset with standard deviation analysed with MetaWin	Datasets with standard deviation analysed with R using bootstrap
Random	-0.28 (-0.48, -0.10) *	-0.08 (-0.33, 0.17)	-0.08 (-0.39, 0.24)
Repeated	-0.16 (-0.26, -0.06) *	-0.15 (-0.34 0.03)	-0.14 (-0.32, 0.04)
Cereal	-0.23 (-0.41, -0.033) *	0.03 (-0.12, 0.06)	-0.10 (-0.40, 0.20)
Root	-0.15 (-0.31, 0.02)	0.01 (-0.21, 0.23)	0.03 (-0.09, 0.14)
All crops	-0.22 (-0.37, -0.07) *	-0.26 (-0.33, -0.20) *	-0.21 (-0.49, 0.06)
Before 1980	-0.24 (-0.36, -0.12)*	-0.13 (-0.27, 0.02)	-0.12 (-0.27, 0.03)
Overlapping 1980	-0.25 (-0.42, -0.08)*	-0.25 (-0.65,0.15)	-0.16 (-0.69, 0.36)
After 1980	0.13 (-0.11, 0.37)	0.43 (0.31,0.54)*	0.43 (0.35, 0.51)*
Null	-0.21 (-0.31, -0.12) *	-0.13 (-0.24 -0.011) *	-0.12 (-0.29, 0.05)

Table 3: General linear model for the whole dataset including crop type (cereal, root, undefined: all), time period (beginning after 1980, ending before 1980, overlapping 1980), latitude, longitude, precipitation and design (random, repeated; see Table 2) on the log response ratio weighted with the area of the study

Coefficients	Estimate	SE	t -value	P-value
Intercept (all, after 1980, random)	-1.065	1.031	-1.034	0.307
Cereal	0.101	0.128	0.791	0.433
Root	0.176	0.160	1.101	0.277
Before 1980	-0.620	0.196	-3.163	0.003
Overlapping 1980	-0.507	0.198	-2.556	0.014
Latitude	0.010	0.019	0.526	0.602
Longitude	0.025	0.012	2.153	0.037
Precipitation	0.001	0.000	1.876	0.067
Repeated	0.190	0.106	1.789	0.080

Table 4: Mixed-effect model for the dataset with standard deviations including crop type (cereal, root, undefined = all), time period (beginning after 1980, ending before 1980, overlapping 1980), longitude, latitude, precipitation and design (random, repeated, see Table 2) on the log response ratio; residual heterogeneity = 0.00, p = 1.00; test of moderators: = 2.41, p = 0.64).

	Estimate	SE	z-value	p-value
Intercept (all, random, after 1980)	3.16	4.41	0.72	0.47
Cereal	0.30	0.31	0.97	0.33
Root	0.56	0.40	1.41	0.16
Before 1980	-0.77	0.46	-1.69	0.09
Overlapping 1980	-0.83	0.47	-1.78	0.08
Latitude	-0.05	0.07	-0.77	0.44
Longitude	-0.02	0.04	-0.55	0.58
Precipitation	0.00	0.00	0.21	0.84
Repeated	-0.27	0.38	-0.70	0.48

Table 5: Traits and the number of times a particular trait was mentioned to positively or negatively influence changes in the numbers of arable weeds in the literature.

Trait	Positive	Negative
Indicator species		13
Tolerant to extreme pH		8
Large seeds		2
Nutrient-loving	14	
Monocotyledon	8	
Herbicide resistance	7	
Neophyte	6	
Ubiquist	4	
Tolerant to minimum tillage	2	
Wind dispersed	2	
Long flowering time	2	
Ruderal	2	1
Rare plant	2	6
Short living seeds	1	1
Long-living seeds	2	1
Shade tolerance	7	3
Moisture-loving	6	1
Small size	2	2
Summer annual	3	3
Temperature-loving	3	1
Winter annual	1	1

Chapter II

Dramatic Decline in the Swiss Arable Flora Since the 1920s

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Abstract

Arable weeds are among the plant groups that are most threatened in Europe, due to agricultural intensification and efficient cleaning of crop seeds. Species loss in arable fields was assessed in many European countries about 30 years ago, but more recent changes in arable weeds have scarcely been evaluated. In Switzerland, a large vegetation database offered a unique opportunity to study changes in arable weed species over the last 90 years. The database contained around 3'500 vegetation surveys from arable land between the 1920s and 1980s. In 2011 and 2012, we re-surveyed 515 of these locations. If the current crop type corresponded with the historical one, we recorded all plant species on plots of 100m^2 and estimated their abundance. Across all plots, species richness did not change significantly, but the mean number of species per plot declined dramatically by over 60%. Most species decreased in frequency, but common species stayed abundant while rare species often disappeared. Species with increasing frequency were mostly neophytes, grasses and species with high nutrient demand. Decreasing species were mostly species characteristic of traditionally managed weed communities. This decline in species number and frequency suggests that more explicit conservation measures have to be taken to ensure the persistence of rare arable weed species.

Keywords: arable weeds, biogeographic regions, functional traits, rare species, segetal flora, Switzerland

Introduction

Arable weeds can be defined as plants which preferably grow in cultivated fields, but are not intentionally sown or planted there. In Europe, arable weeds mainly evolved from Mediterranean plants during the domestication and development of cereal crops during the last 5000 years (Holzner and Immonen, 1982). Arable weeds became attuned to the rhythm of sowing and harvesting (Scholz, 1996). The introduction of new crop species from the new world after 1500 led to an even richer arable flora as their associated weeds were co-introduced (Holzner and Immonen, 1982). By 1950 a very rich arable flora had been assembled in Central Europe, consisting of old elements from southern Europe and newer elements from the Americas. However, during the last 70 years, rapid changes in agricultural practices had a major impact on arable weeds. Today's farming in Europe is characterized by high input of fertilizers and pesticides (Herzog *et al.*, 2006). This results in minimal intra-crop competition for nutrients and a reduction of infestation by noxious weeds, which allows farmers to grow crop plants in higher densities and achieve higher yields, but also negatively affects the accompanying arable flora (Robinson and Sutherland, 2002). Furthermore, as crop seed cleaning became more efficient, seeds of arable weeds are no longer spread on fields via crop seeding (Van Elsen, 1994). The result is that 137 out of 176 arable weeds species became rare and are therefore red listed in Switzerland (Moser *et al.*, 2002; Storkey *et al.*, 2012).

Several studies have examined changes in the arable flora of Europe, but most of them have been carried out in the 1980s (Mahn, 1984; Hilbig, 1987). Mean species number and mean abundance of species in individual fields decreased in the majority of cases (Albrecht and Bachthaler, 1990; Šilc and Čarni, 2005; Baessler and Klotz, 2006). A meta-study on arable species in Central Europe showed a reduction of species per field of 20% to 50% for the period between 1950 and 1990 (Albrecht and Bachthaler, 1990). Rare species are often lost, and weed species that had been rare in a previous survey in Oxfordshire were almost absent 40 years later (Sutcliffe and Kay, 2000).

However, fields which harbored rare species in a historical surveys had a higher probability to still harbor rare species in contemporary surveys (Sutcliffe and Kay, 2000). Since the 1980s, the negative trend in the arable flora is believed to have been slowed, stopped or even reversed due to the implementation of agri-environmental schemes such as field strips or a lower overall input of fertilizers (Decrem *et al.*, 2007). Current species richness in arable fields is roughly 70% of that in 1920s (Richner *et al.*, 2014). Several recent studies from Europe suggested higher overall species richness in arable weeds than in former surveys (Sutcliffe and Kay, 2000; Hyvönen *et al.*, 2003; Šilc and Čarni, 2005; Baessler and Klotz, 2006; Dessaint *et al.*, 2007). However, this higher species number is potentially not due to the former characteristic weed species returning to arable fields, but rather new species such as neophytes (introduced to Switzerland after AD 1500) and pesticide-tolerant species migrating into both cereal and root crop fields (Otte *et al.*, 2006). These processes also led to a homogenization of arable weed communities (Májeková *et al.*, 2010; Meyer *et al.*, 2013). Due to the rich historical dataset and its geographically central position, the patterns in Switzerland may be indicative of the Central European patterns, consequently it is an excellent place to investigate the changes in the segetal flora.

In Switzerland, a list of species important for the Swiss agricultural landscapes has recently been published (BAFU and BLW, 2008). These importand species are representative of the different agricultural habitat types (and are either listed as target (Z) or indicator (L) species. Z-species are only sporadically found in today's fields, are mostly red listed and are thus target species for conservation measures (Walter *et al.*, 2013). L-species are characteristic species of a farmland habitat type and are used for monitoring purposes. Both Z- and L-species should be promoted by agricultural policy and practice in Switzerland (BAFU and BLW, 2008).

By using historical records from an existing large data set of vegetation surveys in arable fields in Switzerland (Volkart, 1933; Buchli, 1936; Salzmann, 1939; Brun-Hool, 1963; Waldis, 1986), we

investigated changes in mean species number across arable weed species, of red listed species and Z- and L-species, of changes in their frequency and local abundance as well as in plant functional traits of arable weed communities. We tested the following two hypotheses. (1) Fewer arable weed species are found in contemporary than historical fields. (2) The composition of weed communities has changed, with ubiquitous species persisting and becoming more frequent and specialist species (in terms of functional traits) disappearing.

Material and methods

Study area

Our study sites were distributed between 245m and 1670 m above sea level across all six biogeographic regions of Switzerland (Gonseth *et al.*, 2001): Jura (JU), Midlands (ML), northern Alps (NA), southern Alps (SA), eastern central Alps (EZA) and western central Alps (WZA). Mean annual temperature in Switzerland across those regions varies between 5.5 °C and 10.5 °C, and mean annual rainfall varies between 545 mm and 1900 mm (MeteoSchweiz, 2013).

Selection of historical relevés and locations for re-survey

The large vegetation database of Agroscope Reckenholz-Tänikon ART in Zürich allowed us to compare the historical and contemporary weed flora in Swiss arable fields. We selected historical plot relevés of wheat, barley, beet or potato fields, other crops were neglected as they were rarely present in the historical surveys. We assigned these datasets to a biogeographic region and further assessed whether the historical relevés contained species that are now red-listed in Switzerland (Moser *et al.*, 2002). Subsequently, we took a stratified random sample of the whole dataset. The strata consisted of biogeographic region, historical author, Red List status and crop type. We selected 700 locations with historical relevés of which we re-surveyed 515 in 2011 and 2012. Locations that now only show grassland on aerial photographs were not visited. For identifying the location of

historical relevés, we relied on the original historical references in combination with spatial analysis in ArcGIS (ESRI). We were able to locate plots with an accuracy between 10m and 500m but more than 50% of the plots had a site specific accuracy of less than 50 m in radius. Hence, our re-survey study corresponds to a semi-permanent plot design (Fig. 3). We only repeated historical relevés if we found the same crop type as in the historical relevés inside the site-specific accuracy-radius. We considered one historical and one contemporary plot per field.

Floristic data

We recorded the floristic composition of contemporary fields in a rectangular plot of 100 m^2. The plots were placed at least 3m from field margins, so the relevés were not influenced by the the field border flora. Plot sizes of historical relevés varied between 4 m^2 and 200 m^2 with a mean of 100.7 ± 4.3 m^2. So we chose a plot area of 100m^2 for the contemporary relevés. We established a species area curve based on the historical data from Brun-Hool (not published, Fig. 4) in order to check whether small plot sizes in historical relevés are problems in the statistical analysis. The minimum area to find over 90% of the species present increased from about 15m^2 in the 1950s to 100m^2 in the 1980s (Fig. 4).

For contemporary relevés we recorded all plant species and estimated their coverage according to the method of Braun-Blanquet (1928) as in the historical relevés. Additional species found in the field margins and volunteer crops were also listed. Nomenclature was based on Aeschimann and Heitz (2005). We made no relevé if a field had already been harvested, temporary ley or if it had changed into built-up or urban area. To ensure that arable weeds were flowering and fields had not yet been harvested, we conducted relevés between April and early September, approximately at the same date at which the historical relevés had been carried out. All contemporary relevés were done by the same person (Nina Richner).

Functional traits

We first established the Red-List status (Moser *et al.*, 2002) and the Z- and L- species status (BAFU and BLW, 2008) of all species recorded. We then analyzed changes in the following functional traits of weed communities: indicator value for light, nutrients and temperature, growth form (herbs, grasses, legumes), life-history (type of seed dispersal: wind dispersed or not wind-dispersed, beginning of flowering), ecological group (forest plant, wetland plant, unfertilized dry meadow plant, weeds and ruderals, fertilized meadow plant, pioneers, other plants), time of introduction to Europe (Idiochrophyte: native or naturally immigrated species; archaeophyte, species introduced before AD 1500; neophyte, species introduced after AD 1500) and geographic distribution (A: outside Europe; B: Europe and other continents; C: more than one continent around the Mediterranean; D: Europe without mountains; E: European Mountains). These functional traits were scored from Landolt *et al.* (2010). Additionally, we noted whether the weed species are characteristic for one of the arable communities of Delarze and Gonseth (2008) (Aphanion, Caucalidion, Polygono-Chenopodionm, Fumaria-euphorbion, Panico-setarion, Eragrostion). Traits and affiliation to a specific arable community are listed for all recorded plants in Appendix A.

Statistical Analysis

All statistical analyses were done in R 3.0 using the package vegan (R Development Core Team, Oksanen *et al.*, 2013; 2013). Taxa that could not be identified to species were included only in analyses on species number, but were excluded from analyses of species composition. To test for differences in mean species number between historical and contemporary plots, in red listed, Z-, L-species as well as in the number of species characteristic for specific arable communities, pairwise, two-tailed Wilcoxon-tests were applied. Composition of functional groups was calculated as the mean percentage of plant species per functional trait (see above) per plot as well as in the overall data set. We calculated general linear models using year and month of relevé, crop type and cover,

biogeographic region, accuracy of localization, contemporary farming practice (organic or integrated production; Eidgenossenschaft, 2014) as explanatory variables and species number per plot as response variable. We selected the best fitting model using Akaike's Information Criterion (AIC) values and sequential likelihood-ratio tests (Burnham and Anderson, 2002). Additionally, we performed a principal component analyses (PCA) to show changes in species composition across time and crop-type.

Results

At the 515 re-visited locations, we made 232 relevés. The remaining locations consisted of 218 temporal leys, meadows or pastures, 26 fields with a crop type varying from the historical one and 26 built areas. In 13 cases, the corresponding field had already been harvested.

A total of 295 arable weed species were recorded in the historical plots but only 214 in contemporary plots When including species from field borders, species number increased to 322 for contemporary fields. In the contemporary plots, we found 48 species which were not present in the historical plots. Most of these new species were common species or neophytes such as *Geranium pyrenaicum* Burm., *Galinsoga ciliata* Blake or *Nicandra physalodes* Gaertn.. In the contemporary plots, we could not confirm 130 species which had been present in the historical plots. Many of these lost species were characteristic species of traditionally managed arable fields such as *Anagallis foemina* Mill*., Papaver argemone* L*., Agrostemma githago* L*., Ajuga chamaepitys* Schreb. or *Legousia speculum-veneris* Chaix.

Average species number per plot decreased significantly from historical to contemporary plots by 66% from 22.7 to 7.9 species (n=232, Wilcoxon: $p_{two\text{-}tailed} < 0.001$). Inclusion of species from field borders increased mean species number per contemporary field by about 13 to 20.4 species; a number that was still significantly lower than for historical plots (Table 1). The total number of red

listed species in the historical plots was 42 compared to 15 in contemporary plots, rising to 20 if species from the field border were included. The number of plots with red listed species in historical and contemporary plots was 121 and 24, respectively. The mean numbers of Red List, Z- and L-species per plot all declined significantly (Table 1). In the contemporary plots we found red list species and species characteristic for arable field communities more often in field borders than in the plots in field centers (Table 1).

The most frequent species in historical plots was *Fallopia convolvulus* Löve. (61.6%), while in contemporary plots it was *Chenopodium album* L. (37.9%, without field borders). Seven of the 15 historically most frequent species were still in the "Top 15" list and all of them were in the "Top 30" list (Table 2). However, the frequency of common species was much higher in historical than in contemporary plots. Today, only 53 species were present in more than ten plots, while historically 107 species occurred in more than ten plots (Fig. 5). Most species that were no longer present in contemporary plots already had a frequency less than 5% in historical plots. Mean species frequency between historical and contemporary plots declined by 52% from 7.7% to 3.7% (Appendix B).

Mean weed cover per field declined by 92% in the last 90 years. The biggest change in weed cover happened between 1935 and 1955 from 89% to 30%. Mean change in weed cover between historical and contemporary plots decreased the more recent the historical data were (Fig. 6). Contemporary plots had a mean weed cover of 5.8% ± 0.8.

Mean species number did not decrease evenly over the six biogeographic regions of Switzerland. While in historical surveys fields in the Jura, Midland and northern Alps had high mean species numbers, currently the Central and Southern Alps have the highest numbers of arable weeds (Table 3. Crop type had no effect on species number in historical or contemporary plots (Table 4).

The proportion of grass species per field increased from 8.3% to 19.4% (n=232, Wilcoxon: $p_{two\text{-}tailed}$ <0.001) during the last 90 years. Weedy grasses did not only increase in number, but they also had a three times higher percentage in the total data set as well as on the plot level, while those of legumes and herbs decreased (Table 5). Comparing historical and contemporary plots, plants characteristic of fertilized meadows increased at the expense of weedy or ruderal species (Fig. 7). Neophytes, nitrophileous, wind dispersed or early flowering species and species with a broad geographic distribution increased as well (Table 5). The percentage of shade-tolerant species per plot declined while that of light-demanding species increased. However, the percentage of light-demanding species in the total data set declined from 58% to 55% (Table 5). The number of species characteristic for arable fields decreased from 9.02 ± 0.4 to 0.57 ± 0.1 per plot (n=232, Wilcoxon: $p_{two\text{-}tailed}$ <0.001) and their total number decreased from 116 to 90 between historical and contemporary plots, respectively.

In a PCA (Fig. 8), no clear difference in community composition between historical and contemporary plots nor between root and cereal crops in either historical nor contemporary plots were detected.

Considering only contemporary fields, weed species number and cover decreased significantly with increasing crop cover, but we found no influence of the recorder of the historical relevés, biogeographic region, time since historical relevés, season of the relevés or accuracy of localization on the number of species found in contemporary relevés

Discussion

We recorded a decline from historic to contemporary plots in total as well as in average weed species number across Switzerland. While historic communities harbored species characteristic for traditionally managed fields, contemporary communities have more neophytes and

monocotyledons. However, the previously most common species are still the most common, even if they decreased in frequency.

Fewer arable weed species in contemporary than historical fields

Our results of a significant decline in mean species number and cover per plot of 65% and 90%, respectively, in arable weeds of fields of Switzerland are in line with a recent study from Germany where the respective decline was of similar order with 70% and 90% (Meyer *et al.*, 2013). With over 75%, the decline in red listed or L-species was even more pronounced in the present study. While many rare or threatened arable weeds have vanished or decreased significantly, decreasing weed species frequency is not necessarily undesirable in cases of noxious weeds such as *Cirsium arvense* Scop. or *Galium aparine* L. (Holzner, 1982). However, while in our study ruderal and weedy species did generally decline, the loss was more pronounced for species characteristic of traditionally managed fields such as *Adonis aestivalis* L. or *Scleranthus annuus* L. This finding is in agreement with many other studies (e.g. Meisel, 1979; Walker *et al.*, 2009; Meyer *et al.*, 2013). The big increase (over 30%) in mean species number per plot as well as in total species number if species from the field border were included, indicates that the field borders serve as a refuge for arable weed species (Fried *et al.*, 2009b).

The observed difference in the change of mean species number of arable fields among biogeographic regions might have resulted from higher intensification of agriculture in the Swiss midlands as compared with mountainous regions in Switzerland such as the central and southern Alps. Yields at higher altitudes are lower and farming is less profitable there and therefore more prone to abandonment (Stöcklin *et al.*, 2007). The few farmers of mountainous regions farm in an organic way or emphasize ecological compensation or conservation areas for which they get subsidies (Eidgenossenschaft, 2014). Additionally, at higher altitudes rapeseed (*Brassica napus* L.; see below), which is used in crop rotation with cereal crops, cannot be grown due to climatic limitations

(Lauber and Wagner, 2001). Hence, the weed flora of cereal fields is less disturbed by crop rotation in mountainous than in lowland regions.

Changing composition of weed communities

Common arable weed species stayed more widespread although their frequency across fields in Switzerland decreased. In contrast, rare species not only became rarer but were even lost. These findings are in line with Sutcliffe and Kay (2000), Smart *et al.* (2005) and Dessaint *et al.* (2007). The persistence of widespread species while rare species are lost results in a homogenization of the arable weed communities (Fried *et al.*, 2010). In accordance with Kühn (1980), Otte *et al.* (2006) and Lososová and Simonová (2008), we found more neophytes in contemporary than in historical plots. On the one hand, this might be due to newly introduced crop species which brought along associated weeds (Holzner and Immonen, 1982). On the other hand, species with a broad geographic distribution also increased in our survey, which was probably due to their wide-spread introduction caused by various human activities (Holzner and Immonen, 1982).

Grass weeds such as *Echinochloa crus-galli* P. B. or *Lolium perenne* L. increased in frequency as well as in their percentage of the species pool. This might be due to broadleaf-selective herbicides. As they were designed to not affect cereals – which are also grasses – grass weeds are not antagonized (Fryer and Chancellor, 1970; Wrucke and Arnold, 1985).

The species that increased most in frequency (*Brassica napus* L.) was rarely cultivated in historical times (BFS, 2013b), but it often occurs as a volunteer crop in contemporary beet-, potato- or cereal fields. Volunteer crops are considered as weeds and can potentially influence the yield and build stable populations (Gulden *et al.*, 2003). Up to now no this was of no concern but should be kept in mind (Simard *et al.*, 2002).

Shade-tolerant species declined while light-demanding species increased from historical to contemporary plots. The literature reports both decreases (Smart *et al.*, 2003; Lososová *et al.*, 2008) and increases (Fried *et al.*, 2009a; Walker *et al.*, 2009) in light-demanding species. Decreases can be explained by higher modern crop density, which results in less light penetration to the ground and consequently a greater competition for light (Austin *et al.*, 1980). Increases can be explained by the fact that today's cereal varieties having shorter stems and more erect leaves leading to more light penetrating to the ground than former cereal varieties allowed (Fossati and Paccaud, 1986). Alternatively, the decline in shade-tolerant species could be explained by the reduction in hedges and small woodlands interspersed among contemporary agricultural fields (Antrop, 2004). As shade-tolerant species can no longer invade fields from such field-edges or wood-lots, they decline in number. However, most weed species characteristic of traditionally managed arable fields are light-demanding species. This discrepancy could be explained by many of the newly occurring weed species which replace the traditional ones, such as *Amaranthus retroflexus* L. or *Galinsoga ciliata* Blake are light-demanding species as well (Landolt *et al.*, 2010).

The clearance of trees and shrubs from farmlands should also increase the number and percentage of wind-dispersed species as there are less barriers to wind-dispersal in present-day agricultural landscapes than they formerly were (Chancellor and Froud-Williams, 1984; Lososová and Simonová, 2008).

Changes in the community composition of arable weeds were most likely due to higher herbicide application and fertilization input as well as different sowing dates. Nitrophileous species increased as fertilizer input is much higher today than it was before the Second World War, even if it is again decreasing since about the 1990s (Decrem *et al.*, 2007; BFS, 2013a). Additionally, contemporary N-input from the atmosphere is also high with 0.1 - 0.7 kg per hectare and year (Vitousek *et al.*, 1997). The decline of early flowering species found in the present study was in line

with other studies on arable weeds and could have been caused by a shift in sowing date from spring to autumn cereals during the last century (Storkey *et al.*, 2013). This decline might thus be due to altered competition during the emerging phase of seedlings. While crop and weeds germinate at around the same time in spring sown crops, crop plants sown in autumn are already well establish during weed-germination in spring and hence are more competitive (Fried *et al.*, 2008).

According to PCA result, we cannot distinguish the floristic composition of contemporary plots from that of historical plots. However, the variation among contemporary plots was distinctly smaller than in the historical plots. This result indicates that contemporary weed communities are more similar to one another than historical ones, i.e. we – as did many other studies - observed a homogenization of weed communities (Tilman *et al.*, 2001; Green *et al.*, 2005; Meyer, 2013). However, as the common species in contemporary plots are still the same as in historical plots, the communities will not separate in a PCA even if the respective species pool is depleted.

Methodological issues

In the historical data set not all information necessary for a detailed analysis of the arable flora was reported. Details on plot size, exact localization and relevé procedure (e.g. if field borders were included) were often missing or fragmentary. However, even if the plot size had been smaller in historical studies, this should not have had an influence on our result as the minimum-area for vegetation plots in arable land increased in the meantime from about 15m^2 for historical plots to about 100m^2 in recent times (Fig. 2; Ellenberg, 1956), and we used a plot size of 100m^2. Even if we additionally included those species that additionally occurred in field borders - aiming for a more conservative estimate of the number of contemporary arable weed species - our result of a general decline of arable weeds did not change.

Not all historical plots could be localized with the same accuracy. We had a high accuracy in the Alps and for more recent surveys because either localization information was good or there were exact coordinates provided by the authors. In the Swiss midlands, localization was sometimes difficult, because altitude and inclination do not change that much in this uniform landscape. However, we found no influence of localization accuracy on change in species number or on community composition, possibly because for those regions where higher deviance could potentially make a large difference, habitat conditions and therefor the arable flora change on a rather small scale (e.g. Alps). In contrast, in the Swiss midlands, the arable flora remains more or less the same across larger spatial extends (Brun-Hool, 1963; Waldis, 1986).

The historical plots were not uniformly dispersed across biogeographic regions in Switzerland nor in time. For example, we had no historical relevés of the south-western or north-eastern part of Switzerland. However, general linear models again suggest that there was no influence of region or time on the number of species recorded in the contemporary plots.

To ensure that the weed community surveyed in the present study was the most similar possible to the historical one, we only considered weed diversity among historical and contemporary plots of the same crop type. As Switzerland has implemented regulated crop rotation, weeds that depend on a certain crop type, will only be able to reproduce every few years (Buchli, 1936; Salzmann, 1939; Eidgenossenschaft, 2014). On the other hand, seeds of arable weeds usually have high longevity (Thompson *et al.*, 1998) and can thus survive in local seed banks for a long time.

Conclusions

The dramatic decline in number and frequency of arable weed species found in this study indicates that more focused conservation measures are necessary to ensure the survival of rare and threatened weed species. Such measures should not only take place in regions where arable weed

diversity is still high (although these regions certainly have priority) but also in nowadays depauperate regions that had a historically rich arable flora and where seeds of arable weeds are still likely to occur in the seed bank. Specific measures in high-diversity regions have already been implemented (e.g. Staatsrat des Kantons Wallis, 1999; Agrofutura, 2012), but more general measures are needed as well. One possibility is to install more, larger and wider unsprayed field borders or to use seed mixtures for establishing arable production-systems which promote rare weeds. Nevertheless, one has to be aware of several problems with such measures. First, seed-mixtures of arable weeds sown in ecological compensation areas may contain non-adapted non-regional genotypes (Vander Mijnsbrugge *et al.*, 2010). Second, not all arable weeds are favorable. There are some species which grow in high densities, are resistant to herbicides and may lead to lower crop yields. In order to ensure production, farmers need to keep track of such possibly harmful weeds such as *Apera spica-venti* L.*, Elymus repens* Gould*, Alopecurus myosuroides* Hud.s*, Galium aparine* L. or *Cirsium arvense* Scop..

In future studies, it would be advantageous to sample fields of oilseed-rape, corn and other crop-species, to see if rare species do also occur there, as they have rarely been survey for weed diversity. Conservation ecology is often perceived in a conservative way, but it would be valuable to search for “new” arable communities in which the rare weed species could survive. On the other hand, it would also be advantageous to get an overview of the whole range of modern arable weed communities, which are heavily invaded by newly introduced species.

The increase in number and frequency of newly introduced arable species could pose new chances but also new risks for production and nature conservation. There could be a loss of yield due to invasive species but also new food resources for beneficial organisms. As arable fields are a highly and regularly disturbed habitat, changes in floristic composition of weeds happen fast and trends can be detected rapidly.

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Figures

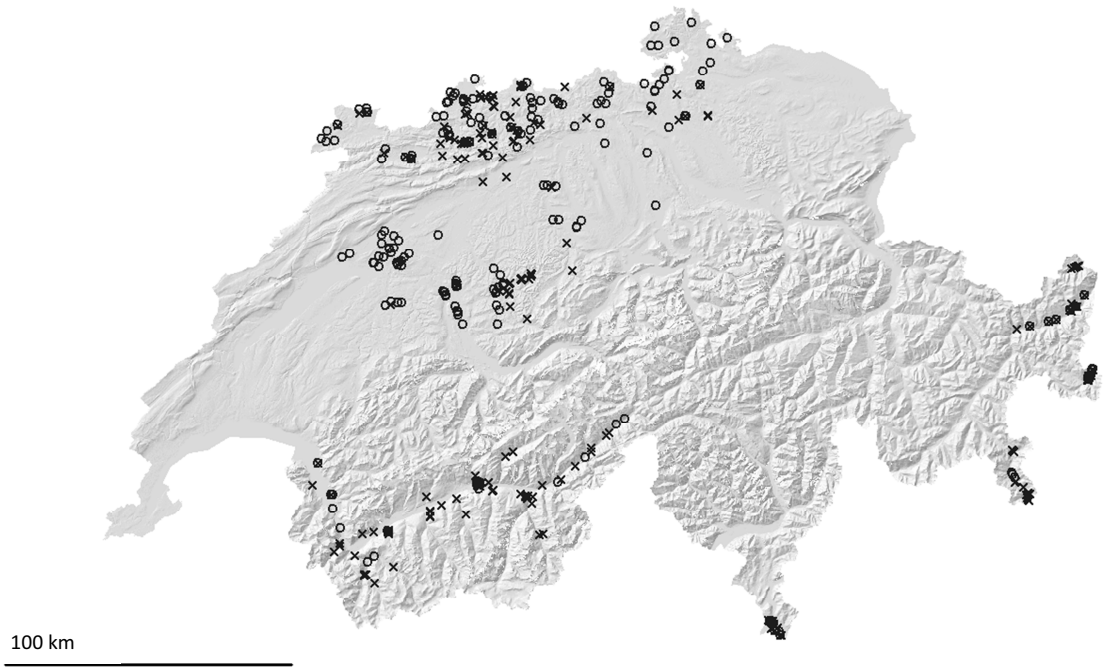

Fig. 3: Map of all re-visited locations in Switzerland. At locations marked with circles contemporary arable weed community was recorded, at those marked with crosses, arable communities could not be recorded.

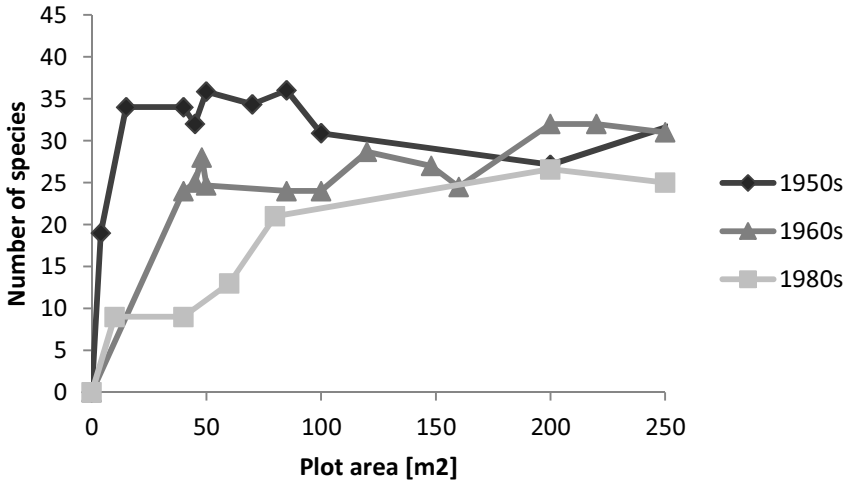

Fig. 4: Species area curves for arable weed plots from the 1950s, 1960s and 1980s based on data from Brun-Hool (not published).

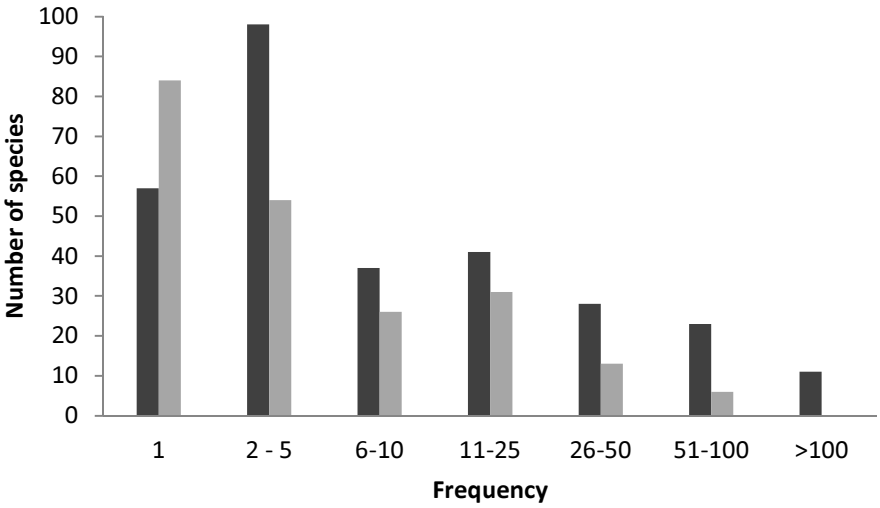

Fig. 5: Frequency of arable weed species in historical (dark grey) and contemporary (light grey, n=232) plots.

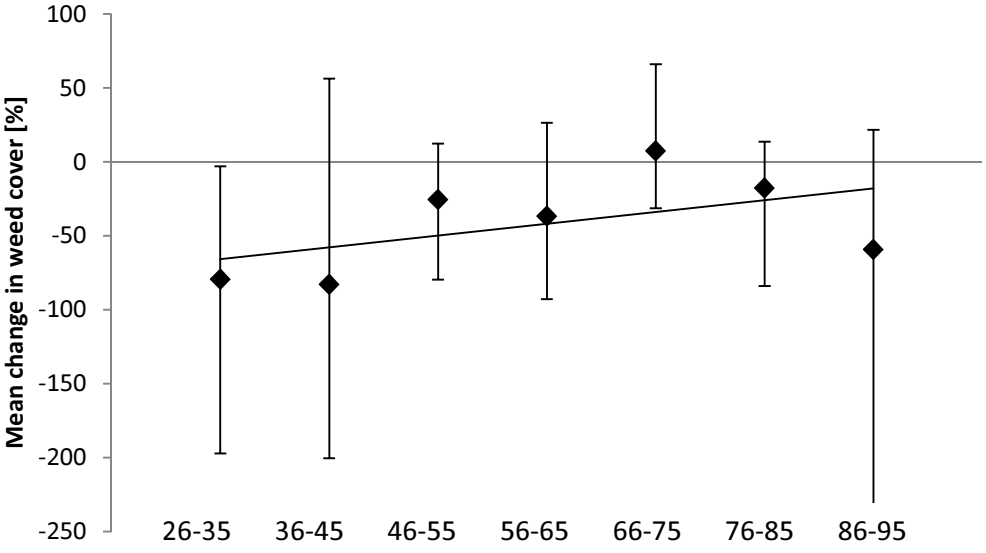

Fig. 6: Mean change in arable weed cover per plot between historical and contemporary plots. Historical plots were split into seven temporal groups of ten years starting in 1926. Bars mark minimum and maximum change. (n_{26-35}= 76, n_{36-45}= 77, n_{46-55}= 9, n_{56-65}= 33, n_{66-75}= 6, n_{76-85}= 23, n_{86-95}= 8, R^2=0.266)

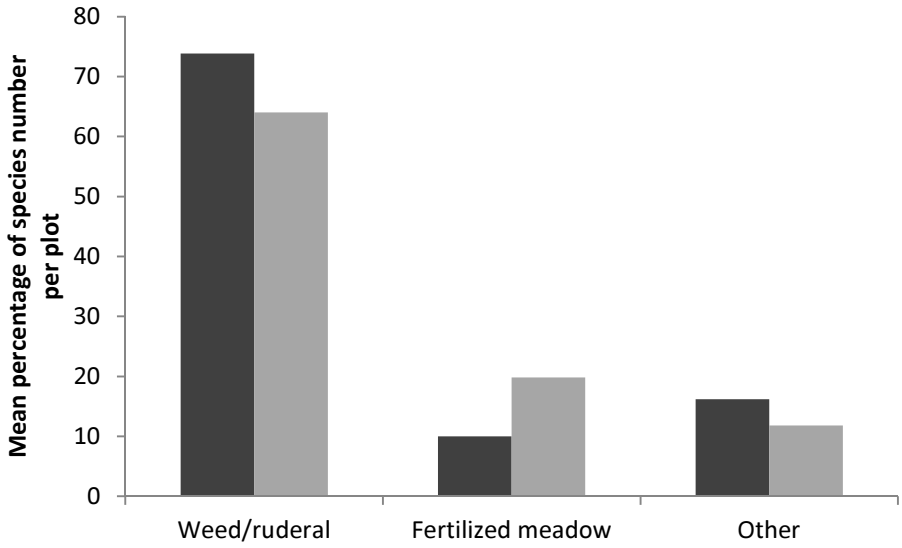

Fig. 7: Mean percentage of number of species per plot in historical (dark grey) and contemporary (light grey) surveys of arable weeds in groups of species characteristic for particular habitats. (other=plants of wetland, forest, unfertilized meadow or from the mountains).

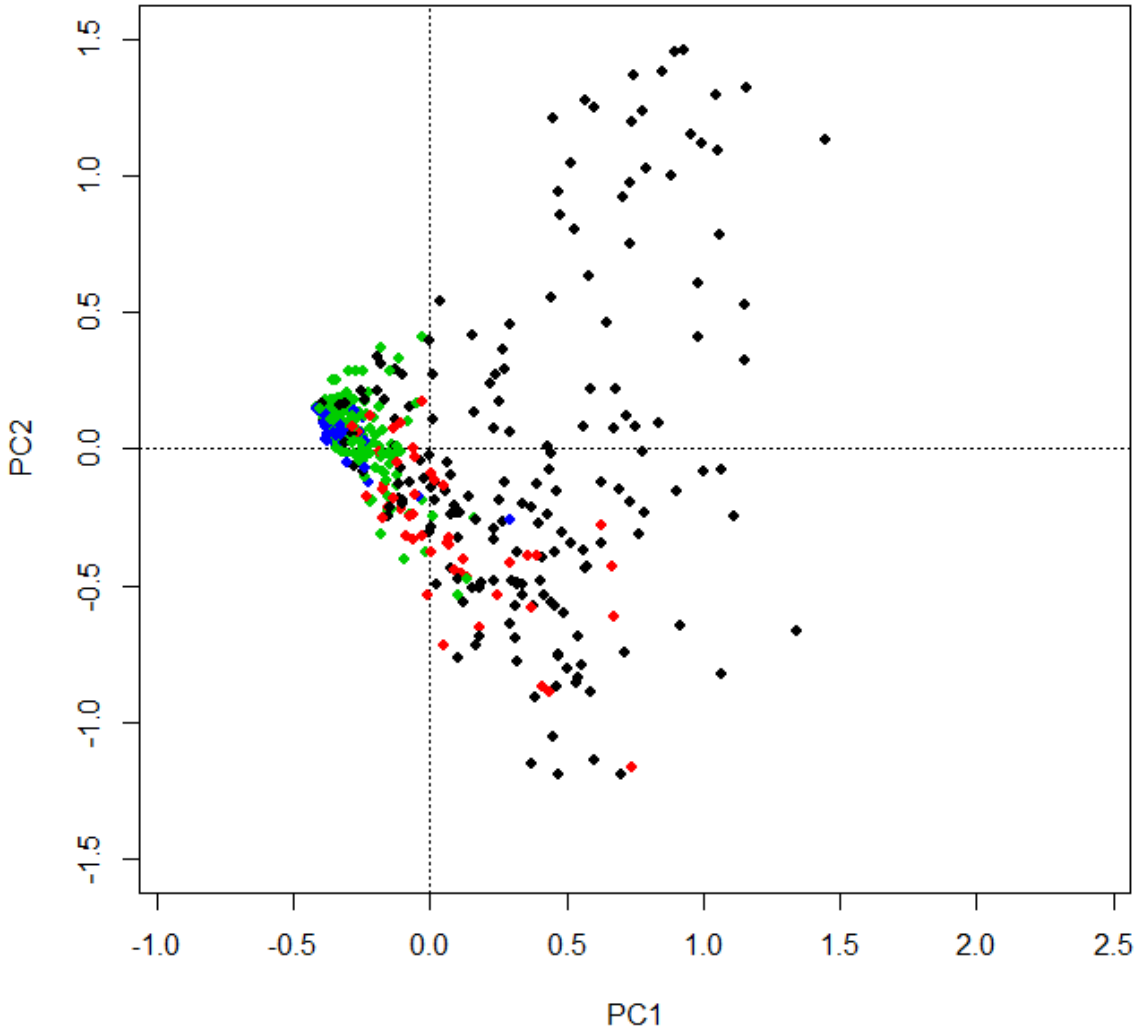

Fig. 8: PCA showing historical and contemporary plots of arable weeds in cereal and root crop fields. Black dots: historical cereal plots, red dots: historical root crop plots, green dots: contemporary cereal plots, blue dots: contemporary root crop plots. The first axis explains 12.8% of the total variation, the second axis 8.4%.

Tables

Table 1: Total species number and mean species number per plot of historical and contemporary plots (n=232) for all weed species (with plants of field borders either included or not included), Red List species (Moser et al., 2002), Z- and L- species (see text; (Walter et al., 2013) and characteristic species for arable communities (Delarze & Gonseth, 2008).

	Total historical number	Mean historical number per plot	Total Contemporary number	Mean contemporary number per plot	Total contemporary number with borders	Mean contemporary number with borders
All Species	295	22.68 ± 0.53	214	7.86 ± 0.47	322	20.43 ± 0.42
Red List species	43	0.97 ± 0.08	15	0.22 ± 0.05	20	0.40 ± 0.08
Z-species	34	0.87 ± 0.08	15	0.22 ± 0.05	19	0.38 ± 0.07
L-species	92	4.94 ± 0.18	55	0.94 ± 0.1	98	2.86 ± 0.18
Characteristic species	111	12.06 ± 0.35	59	3.44 ± 0.21	92	8.69 ± 0.27

Table 2: The fifteen most frequent species (percentage of occupied plots; total n =232) in historical and contemporary plots. Frequencies of the fifteen most frequent historical and contemporary species are given in bold.

Species	Historical	Contemporary
***Agropyron repens* (L.) P. Beauv.**	37.5	**21.6**
***Anagallis arvensis* L.**	**37.9**	2.6
***Capsella bursa-pastoris* (L.) Medik.**	**41.8**	12.5
***Chenopodium album* L.**	**57.8**	**37.9**
***Cirsium arvense* (L.) Scop.**	**38.4**	9.1
***Convolvulus arvensis* L.**	**47.4**	14.2
***Echinochloa crus-galli* (L.) P. Beauv.**	2.6	**16.8**
***Fallopia convolvulus* (L.) Á. Löve**	**61.6**	**22.8**
***Galeopsis tetrahit* L.**	**50.9**	13.4
***Galium aparine* L.**	**46.6**	12.1
***Lolium multiflorum* Lam.**	4.3	**20.3**
***Lolium perenne* L.**	5.6	**21.1**
***Myosotis arvensis* Hill**	**56.9**	6.9
***Poa trivialis* L.**	**40.5**	**24.6**
***Polygonum aviculare* L.**	**59.1**	**32.8**
***Polygonum persicaria* L.**	**44.4**	**14.7**
***Ranunculus repens* L.**	**57.3**	9.9
***Stellaria media* (L.) Vill.**	34.1	**14.7**
***Taraxacum officinale* aggr.**	**49.1**	**35.8**
***Trifolium repens* L.**	33.2	**15.5**
***Veronica persica* Poir.**	28.4	**29.7**
***Viola arvensis* Murray**	**56.0**	**17.2**

Table 3: Mean number of weed species per plot (with standard error SE) per biogeographic region and historical or contemporary plots

Biogeographic region	n	Point in time	Mean number of species	SE
Jura	43	Historical	27.37	1.16
		Contemporary	6.81	1.08
Midlands	120	Historical	24.53	0.66
		Contemporary	6.34	0.50
northern Alps	20	Historical	19.85	1.17
		Contemporary	7.00	1.04
Eastern Central Alps	18	Historical	17.00	0.73
		Contemporary	13.33	1.36
Southern Alps	8	Historical	17.25	1.25
		Contemporary	14.75	2.21
Western Central Alps	23	Historical	13.09	1.47
		Contemporary	11.87	1.26

Table 4: Results from the best general linear model on species number of arable weeds (ΔAIC: 30), (ML: Midlands, NA: northern Alps, EZA: eastern central Alps, SA: southern Alps, WZA: western central Alps. ***: p< 0.001, **: p< 0.01, ns: not significant

	Estimate	SE	z-value	
Intercept	3.308633	0.029822	110.946	***
Contemporary	-1.378829	0.065806	-20.953	***
Historical: root-crop	0.004781	0.033749	0.142	ns
Contemporary: root-crop	-0.123077	0.063828	-1.928	ns
Historical: ML	-0.109837	0.034573	-3.177	**
Contemporary: ML	-0.05496	0.069215	-0.794	ns
Historical: NA	-0.322105	0.058303	-5.525	***
Contemporary: NA	0.085505	0.108695	0.787	ns
Historical: EZA	-0.47542	0.064477	-7.373	***
Contemporary: EZA	0.660464	0.087223	7.572	***
Historical: SA	-0.460821	0.090198	-5.109	***
Contemporary: SA	0.76144	0.109159	6.976	***
Historical: WZA	-0.73785	0.064591	-11.423	***
Contemporary: WZA	0.585288	0.085472	6.848	***

Table 5: Mean percentage (with standard error SE) of the number of species per plot of different functional groups in arable weeds in historical and contemporary surveys. (n=232). ***: p< 0.001, **: p< 0.01, *: p< 0.05

	Historical	SE	Contemporary	SE	
Neophytes	10.7	0.46	25.1	1.49	***
Nitrophileous	54.4	0.98	68.0	1.76	***
Shade-tolerant	31.2	0.74	21.5	1.34	***
Light demanding	61.6	0.83	64.8	1.72	**
Wind dispersed	20.5	0.57	25.4	1.65	*
Broad geographical distribution	53.2	0.80	58.5	0.68	***
Early flowering	45.8	0.82	41.8	1.72	**
Legumes	7.08	0. 36	2.84	0. 37	***
Grasses	9.57	0. 49	31.14	2.04	***
Herbs	83.35	0.63	66.00	1.98	***

Appendices

Appendix A: Functional traits used for arable weed species recorded. RL: regionally extinct (RE), critically endangered (CR), endangered (EN), vulnerable (VU), nearly threatened (NT), least concern (LC), data deficient (DD), not evaluated (NE); UZL: target (Z) or keystone (L) species (BAFU & BLW, 2008), ecological group: 1: forest plant; 2: mountain plant; 3: pioneer of the lowland; 4: water plant; 5: wetland plant; 6: unfertilized dry meadow plant; 7: weed or ruderal plant; 8: fertilized meadow plant; - : not listed. Introduction: I: idiochrophyt: native or naturally immigrated species; A: archaeophyt, species introduced before AD 1500; N: neophyte, species introduced after AD 1500. Spread: A: outside Europe; B: Europe and other continents; C: more than one continent around the Mediterranean; D: Europe without mountains; E: European Mountains. Characteristic species: yes or no, based on the list for arable weed communities in Delarze and Gonseth (2008). L: indicator value for light, T: indicator value for temperature, N: indicator value for nutrients. Data for ecological group, introduction, spread, indicator values, first month of flowering from Landolt et al. (2010).

Species name	RL	UZL	Ecological group	Introduction	Spread	Life-form	Seed dispersal by wind	First month of flowering	Characteristic species	L	T	N	Annual
***Achillea millefolium* aggr.**	LC		-	I	B	herb	yes	5	no	4	3	3	no
***Acinos arvensis* (Lam.) Dandy**	LC	L	6	I	C	herb	no	6	no	4	4	1	no
***Adonis aestivalis* L.**	VU	Z	7	I	B	herb	no	5	yes	3	5	2	yes
***Adonis flammea* Jacq.**	EN	Z	7	I	C	herb	no	5	yes	3	5	2	yes
***Aegopodium podagraria* L.**	LC		1	I	B	herb	no	5	no	2	3	4	no
***Aethusa cynapium* L.**	LC	L	7	I	B	herb	yes	6	yes	3	3	4	no
***Agropyron intermedium* (Host) P. Beauv.**	LC		3	I	B	grass	no	5	no	4	4	3	no
***Agropyron repens* (L.) P. Beauv.**	LC		7	I	B	grass	no	6	no	4	3	4	no
***Agrostemma githago* L.**	VU	Z	7	A	C	herb	no	6	yes	4	3	3	no
***Agrostis capillaris* L.**	LC		8	I	B	grass	yes	6	no	3	3	2	no
***Agrostis stolonifera* L.**	LC		5	I	B	grass	no	6	no	4	3	3	no
***Ajuga chamaepitys* (L.) Schreb.**	NT	L	7	I	C	herb	no	5	yes	4	4	2	no
***Ajuga reptans* L.**	LC		8	I	B	herb	no	4	no	3	3	3	no
***Alchemilla vulgaris* aggr.**	LC		-	I	B	herb	yes	5	no	3	2	4	no
***Alopecurus myosuroides* Huds.**	LC	L	7	A	B	grass	yes	5	yes	4	5	3	yes
***Alopecurus pratensis* L.**	LC		8	I	B	grass	yes	5	no	4	3	4	no
***Alyssum alyssoides* (L.) L.**	LC	L	6	I	C	herb	yes	4	no	4	4	2	no
***Amaranthus blitum* L.**	LC		7	I	C	herb	no	7	yes	4	4	4	yes

Species name	RL	UZL	Ecological group	Introduction	Spread	Life-form	Seed dispersal by wind	First month of flowering	Characteristic species	L	T	N	Annual
***Amaranthus hypochondriacus* L.**	LC		-	N	A	herb	no	7	no	4	4	4	yes
***Amaranthus retroflexus* L.**	LC		7	N	A	herb	no	7	yes	4	4	4	yes
***Anagallis arvensis* L.**	LC	L	7	A	C	herb	yes	6	yes	4	4	3	yes
***Anagallis foemina* MilL.**	NT	L	7	A	C	herb	yes	6	yes	3	4	3	yes
***Anagallis minima (*L.) E. H. L. Krause**	EN	Z	7	I	B	herb	yes	6	no	4	4	2	no
***Anchusa arvensis* (L.) M. Bieb.**	LC	L	7	A	C	herb	no	5	yes	4	4	4	no
***Androsace maxima* L.**	CR	Z	7	I	B	herb	yes	4	yes	4	5	3	yes
***Anthemis arvensis* L.**	VU	Z	7	I	C	herb	no	5	yes	4	4	4	yes
***Anthemis cotula* L.**	VU		7	A	C	herb	no	5	yes	4	4	3	yes
***Anthemis tinctoria* L.**	NT		7	I	C	herb	no	6	no	4	5	2	no
***Anthriscus sylvestris* (L.) Hoffm.**	LC		8	I	D	herb	no	4	no	3	3	4	no
***Apera spica-venti (*L.) P. Beauv.**	LC		7	A	B	grass	yes	6	yes	3	4	4	no
***Aphanes arvensis* L.**	NT	L	7	I	C	herb	yes	4	yes	3	4	3	yes
***Arabidopsis thaliana* (L.) Heynh.**	LC		7	I	C	herb	yes	3	yes	4	3	3	no
***Arctium lappa* L.**	LC	L	7	I	B	herb	no	7	no	3	4	5	no
***Arenaria serpyllifolia* L.**	LC	L	7	I	D	herb	yes	5	no	4	4	3	no
***Arrhenatherum elatius (*L.) J. & C. Presl**	LC		8	J	C	grass	yes	6	no	3	4	4	no
***Artemisia absinthium* L.**	LC	L	7	I	B	herb	no	7	yes	4	4	4	no
***Artemisia verlotiorum* Lamotte**	LC		7	N	A	herb	yes	9	no	4	4	4	no
***Artemisia vulgaris* L.**	LC		7	I	B	herb	yes	7	no	4	4	4	no
***Atriplex patula* L.**	LC		7	A	B	herb	no	7	yes	4	3	4	yes
***Avena fatua* L.**	NT		7	A	C	grass	yes	6	no	4	4	3	yes
***Avena sativa* L.**	LC		7	J	C	grass	no	6	no	4	4	4	yes
***Bellis perennis* L.**	LC		8	I	B	herb	yes	2	no	4	3	4	no
***Bifora radians* M. Bieb.**	CR		7	A	B	herb	yes	5	yes	4	5	4	yes
***Brassica napus* L.**	LC		7	J	C	herb	yes	4	no	4	4	4	no
Brassica rapa* L. *subsp.	VU		7	A	d	herb	yes	4	yes	4	3.	4	yes

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***campestris* (L.) A. R. Clapham**											5		
***Bromus arvensis* L.**	VU	Z	7	A	B	grass	yes	6	yes	3	4	3	yes
***Bromus hordeaceus* L.**	LC		8	J	B	grass	no	5	no	4	4	4	yes
***Bromus racemosus* L. *subsp. commutatus* (Schrad.) Syme**	VU		7	A	C	grass	yes	5	no	3	4	3	yes
***Bromus secalinus* L.**	EN	Z	7	J	D	grass	yes	6	no	3	4	3	yes
***Bromus squarrosus* L.**	LC	L	7	N	A	grass	yes	5	no	4	4	4	yes
***Bromus sterilis* L.**	LC		7	A	B	grass	yes	5	no	3	4	4	yes
***Buglossoides arvensis* (L.) I. M. Johnst.**	LC	L	7	I	B	herb	no	4	yes	3	4	4	no
***Bunium bulbocastanum* L.**	LC	L	6	I	D	herb	yes	6	yes	4	4	2	no
***Bupleurum rotundifolium* L.**	EN	Z	7	A	C	herb	yes	5	yes	4	5	2	yes
***Calystegia sepium (*L.) R. Br.**	LC		7	I	B	herb	no	6	no	3	4	4	no
***Camelina microcarpa* DC.**	VU	Z	7	A	B	herb	yes	5	yes	4	4	3	no
***Campanula rapunculoides* L.**	LC	L	3	I	B	herb	yes	6	no	3	4	3	no
***Campanula rapunculus* L.**	LC	L	6	I	B	herb	yes	5	no	3	4	3	no
***Capsella bursa-pastoris* (L.) Medik.**	LC		7	I	C	herb	no	3	yes	4	3	4	no
***Cardamine hirsuta* L.**	LC		7	A	C	herb	no	3	yes	4	4	4	no
***Carex hirta* L.**	LC		7	I	D	grass	yes	4	no	3	4	3	no
***Carum carvi* L.**	LC		8	I	B	herb	no	5	no	4	3	3	no
***Caucalis platycarpos* L.**	VU	Z	7	A	C	herb	no	5	yes	3	5	2	yes
***Centaurea cyanus* L.**	NT	L	7	I	C	herb	yes	6	yes	4	4	3	no
Centaurea jacea* L. *subsp. jacea	LC	L	8	I	D	herb	no	6	no	4	3	3	no
Centaurea scabiosa* L. *subsp. scabiosa	LC	L	6	I	B	herb	no	6	no	4	4	2	no
***Centaurium pulchellum* (Sw.) Druce**	VU	Z	5	I	B	herb	yes	6	no	4	4	3	no
***Cerastium arvense* L. *subsp. strictum (*W. D. J. Koch) Schinz & R. Keller**	LC		2	I	E	herb	yes	6	no	5	2	2	no
Cerastium fontanum	LC		8	I	B	herb	yes	4	no	3	3	3	no

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Baumg. *subsp. vulgare* (Hartm.) Greuter & Burdet													
Cerastium glomeratum Thuill.	LC	L	7	I	C	herb	yes	4	yes	4	3	3	no
Chaenorrhinum minus (L.) Lange	LC		7	A	C	herb	yes	6	yes	4	4	4	yes
Chaerophyllum aureum L.	LC	L	8	I	B	herb	yes	6	no	3	3	4	no
Chaerophyllum hirsutum L.	LC		8	I	E	herb	yes	5	no	3	3	4	no
Chenopodium album L.	LC		7	A	B	herb	no	7	yes	4	3	4	yes
Chenopodium hybridum L.	LC	L	7	A	B	herb	no	7	yes	4	4	4	yes
Chenopodium polyspermum L.	LC		7	A	B	herb	no	7	yes	4	4	4	yes
Chondrilla juncea L.	NT	L	6	I	B	herb	yes	6	no	4	5	3	no
Cichorium intybus L.	LC	L	7	A	B	herb	yes	7	no	5	4	3	no
Cirsium arvense (L.) Scop.	LC		7	I	B	herb	yes	7	no	3	4	4	no
Clinopodium vulgare L.	LC	L	6	I	B	herb	yes	7	no	4	4	2	no
Consolida regalis Gray	VU	Z	7	A	C	herb	yes	6	yes	3	4	3	yes
Convolvulus arvensis L.	LC		7	A	B	herb	no	6	yes	4	4	3	no
*Conyza canadensis (*L.) Cronquist	LC		7	N	A	herb	yes	7	yes	4	4	3	no
Cornus sanguinea L.	LC		1	I	D	herb	no	5	no	3	4	3	no
Crepis capillaris Wallr.	LC		8	I	D	herb	yes	6	n	4	4	3	no
Crepis tectorum L.	VU	Z	7	I	B	herb	yes	6	no	4	4	4	no
*Cynodon dactylon (*L.) Pers.	LC		7	N	A	grass	yes	7	no	4	5	3	no
Dactylis glomerata L.	LC		8	I	B	grass	no	5	no	3	4	4	no
Daucus carota L.	LC	L	6	A	C	herb	no	6	no	4	4	2	no
Descurainia sophia (L.) *Prantl*	LC	L	7	I	B	herb	yes	4	no	4	3	4	no
Dianthus carthusianorum L.		L	6	I	D	herb	yes	6	no	4	3	2	no
Digitaria ischaemum (Schreb.) Muhl.	LC		7	A	B	grass	no	7	yes	4	4	4	yes
Digitaria sanguinalis (L.) Scop.	LC		7	A	B	grass	no	7	yes	4	4	4	yes
Dipsacus fullonum L.	LC	L	7	J	C	herb	no	7	no	4	4	4	no

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*Echinochloa crus-galli (*L.) P. Beauv.	LC		7	A	A	grass	no	7	yes	3	4	5	yes
Echium vulgare L.	LC	L	6	I	B	herb	yes	5	no	5	4	4	no
Epilobium angustifolium L.	LC		3	I	B	herb	yes	6	no	4	3	4	no
Epilobium hirsutum L.	LC	L	5	I	B	herb	yes	6	no	3	4	4	no
Epilobium tetragonum L. *subsp. tetragonum*	LC	L	5	I	B	herb	yes	7	no	3	4	3	no
Equisetum arvense L.	LC		7	I	B	herb	yes	3	no	4	3	3	no
Equisetum telmateia Ehrh.	LC		1	I	B	herb	yes	3	no	3	3	3	no
Erigeron acer L. *subsp. acer*	LC		3	I	B	herb	yes	6	no	5	4	2	no
*Erigeron annuus (*L.) Pers. *subsp. annuus*	LC		7	N	A	herb	yes	6	no	4	4	4	no
Erodium cicutarium (L.) L'Hér.	LC	L	7	I	C	herb	no	3	yes	4	4	3	no
Erophila verna (L.) Chevall.	LC		7	I	B	herb	yes	2	no	4	4	2	yes
*Erucastrum gallicum (*Willd.) O. E. Schulz	NT	L	7	I	D	herb	yes	5	yes	4	5	2	no
Erysimum cheiranthoides L.	NT	L	7	I	B	herb	yes	6	yes	4	4	4	no
Erysimum repandum L.	CR		7	I	B	herb	yes	4	no	4	5	4	yes
Euphorbia cyparissias L.	LC	L	6	I	B	herb	no	4	no	4	3	2	no
Euphorbia exigua L.	LC	L	7	A	C	herb	no	5	yes	4	5	4	yes
Euphorbia helioscopia L.	LC		7	A	C	herb	no	4	no	4	4	4	yes
Euphorbia lathyris L.	NT		7	N	C	herb	no	6	no	3	5	3	no
Euphorbia peplus L.	LC		7	A	B	herb	no	6	yes	4	4	4	yes
Euphorbia platyphyllos L.	LC	L	1	I	C	herb	no	6	yes	3	4	3	yes
Euphorbia stricta L.	LC	L	1	I	B	herb	no	5	no	3	4	3	no
Euphrasia rostkoviana Hayne	LC		5	I	D	herb	yes	5	no	3	2	0	no
Fagopyrum esculentum Moench	NT		7	A	B	herb	no	7	no	4	3	4	yes
Fallopia convolvulus (L.) Á. Löve	LC		7	A	C	herb	no	7	yes	4	4	3	yes
Festuca arundinacea Schreb. *subsp. arundinacea*	LC		5	I	B	grass	no	5	no	4	3	4	no

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***Festuca pratensis* Huds.**	LC		8	I	B	grass	no	5	no	3	4	0	no
***Festuca rubra* L.**	LC		8	I	B	grass	no	5	no	3	3	0	no
Fumaria officinalis* L. *subsp. officinalis	LC		7	A	C	herb	no	4	yes	4	3.5	4	yes
***Fumaria schleicheri* Soy.-Will.**	VU	Z	7	A	B	herb	no	5	yes	3	4	4	yes
***Gagea villosa* (M. Bieb.) Sweet**	EN	Z	7	I	C	herb	yes	3	no	4	4	4	no
***Galeopsis angustifolia* Hoffm.**	NT		3	I	D	herb	no	6	no	4	4	2	no
***Galeopsis ladanum* L.**	NT	L	7	I	B	herb	no	6	yes	4	2	2	no
***Galeopsis tetrahit* L.**	LC		7	I	D	herb	no	6	no	3	3	5	yes
***Galinsoga ciliata (*Raf.) S. F. Blake**	LC		7	N	A	herb	no	7	yes	4	4	4	yes
***Galinsoga parviflora* Cav.**	LC		7	N	A	herb	no	4	no	4	4	4	yes
***Galium aparine* L.**	LC		7	I	B	herb	no	5	no	3	4	5	yes
***Galium mollugo* L.**	LC		1	I	D	herb	no	5	no	3	4	4	no
***Galium spurium* L.**	NT	L	7	I	B	herb	no	5	no	3	4	5	yes
***Galium tricornutum* Dandy**	EN	Z	7	I	C	herb	no	6	yes	4	5	4	yes
***Geranium columbinum* L.**	LC	L	7	A	B	herb	no	5	yes	4	4	3	yes
***Geranium dissectum* L.**	LC	L	7	A	B	herb	no	6	yes	4	4	3	yes
***Geranium molle* L.**	LC	L	7	I	B	herb	no	5	no	4	4	4	no
***Geranium pusillum* L.**	LC	L	7	A	B	herb	no	5	yes	4	4	4	no
***Geranium pyrenaicum* Burm. f.**	LC		7	I	E	herb	no	5	no	3	4	4	no
***Geranium rotundifolium* L.**	LC	L	7	A	C	herb	no	6	yes	4	4	3	no
Glechoma hederacea* L. *subsp. hederacea	LC		8	I	B	herb	no	4	no	3	4	3	no
***Gnaphalium uliginosum* L.**	NT	L	7	I	B	herb	yes	6	no	4	4	4	yes
***Gypsophila muralis* L.**	EN		7	I	B	herb	yes	7	no	4	4	1	yes
***Helianthus annuus* L.**	LC		7	N	A	herb	no	7	no	4	5	4	yes
Heracleum sphondylium* L. *subsp. sphondylium	LC		8	I	D	herb	yes	6	no	3	3	4	no
***Hieracium lactucella* Wallr.**	LC	L	6	I	D	herb	yes	5	no	4	3	2	no

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***Holcus lanatus* L.**	LC		8	I	D	grass	yes	5	no	4	3	3	no
***Holcus mollis* L.**	LC		7	I	D	grass	yes	6	no	3	3	2	no
***Holosteum umbellatum* L.**	LC	L	7	I	C	herb	yes	3	yes	4	5	3	yes
***Hordeum vulgare* L.**	LC		7	J	A	grass	no	3	no	4	4	3	yes
***Hypericum humifusum* L.**	LC	L	7	I	D	herb	yes	6	no	3	3	3	no
Hypericum perforatum* L. *subsp. perforatum	LC	L	6	I	B	herb	yes	6	no	3	4	3	no
***Isatis tinctoria* L.**	LC	L	7	I	B	herb	yes	4	no	4	4	2	no
***Juglans regia* L.**	LC		1	A	C	herb	no	5	no	3	5	4	no
***Juncus bufonius* L.**	LC	L	5	I	B	grass	yes	6	no	4	3	3	yes
***Kickxia elatine (*L.) Dumort.**	VU	Z	7	A	C	herb	no	7	yes	4	5	3	yes
***Kickxia spuria* (L.) Dumort.**	VU	Z	7	A	C	herb	no	7	yes	4	5	4	yes
***Knautia arvensis* (L.) Coult.**	LC	L	8	I	B	herb	no	5	no	4	4	3	no
***Knautia dipsacifolia* Kreutzer**	LC	L	1	I	E	herb	no	6	no	3	3	0	no
***Lactuca perennis* L.**	LC	L	6	I	D	herb	yes	5	no	5	4	2	no
***Lactuca serriola* L.**	LC		7	I	B	herb	yes	7	no	4	5	3	no
***Lamium album* L.**	LC	L	7	I	B	herb	no	5	no	3	4	5	no
***Lamium amplexicaule* L.**	LC	L	7	I	B	herb	no	3	yes	4	3	4	no
***Lamium maculatum* L.**	LC		7	I	D	herb	no	4	no	3	3	4	no
***Lamium purpureum* L.**	LC		7	A	C	herb	no	2	yes	4	3	4	no
***Lapsana communis* L.**	LC		1	I	B	herb	yes	6	no	4	4	0	no
***Lathyrus pratensis* L.**	LC	L	-	I	B	legume	no	6	no	3	4	3	no
***Lathyrus tuberosus* L.**	VU	Z	7	A	A	legume	no	6	yes	4	4	3	no
***Legousia speculum-veneris (*L.) Chaix**	VU	Z	7	A	C	herb	yes	6	yes	4	4	3	yes
***Lepidium campestre (*L.) R. Br.**	LC	L	7	I	B	herb	yes	4	yes	4	3	4	no
***Leucanthemum vulgare* Lam.**	LC		-	I	B	herb	yes	5	no	4		3	no
***Linaria vulgaris* Mill.**	LC	L	7	I	B	herb	yes	6	no	4	4	3	no
***Lolium multiflorum* Lam.**	LC		8	N	C	grass	yes	6	no	4	4	4	no

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***Lolium perenne* L.**	LC		8	I	B	grass	yes	5	no	4	3	4	no
***Lolium temulentum* L.**	CR	Z	7	A	C	grass	yes	6	yes	3	4	4	yes
Lotus corniculatus* L. *subsp. corniculatus	LC		8	I	B	legume	no	5	no	3	3	0	no
***Lysimachia nummularia* L.**	LC		1	I	D	herb	no	6	no	2	4	4	no
***Lythrum salicaria* L.**	LC		5	I	B	herb	yes	6	no	3	4	3	no
***Matricaria discoidea* DC.**	LC		7	N	A	herb	no	5	no	4	4	5	yes
***Matricaria recutita* L.**	LC		7	I	C	herb	no	5	yes	4	3	1	no
***Medicago lupulina* L.**	LC	L	8	A	C	legume	no	5	no	3	4	3	no
***Medicago minima (*L.) L.**	LC	L	6	I	C	legume	no	5	no	4	4	2	no
***Medicago sativa* L.**	LC		8	A	C	legume	no	6	no	4	4	3	no
***Melampyrum arvense* L.**	VU	Z	7	I	B	herb	no	6	yes	4	4	3	yes
***Melilotus officinalis* (L.) Lam.**	LC		7	A	B	legume	yes	6	no	4	4	3	no
***Mentha arvensis* L.**	LC	L	7	I	B	herb	no	7	yes	4	4	4	no
***Mercurialis annua* L.**	LC	L	7	A	B	herb	no	5	yes	4	4	4	no
Miscanthus sinensis	NE		-	N	A	grass	yes	8	no	4	4	4	no
***Muscari comosum* (L.) Mill.**	LC		7	I	C	herb	yes	4	no	4	4	3	no
***Muscari racemosum* (L.) Mill.**	NT	L	7	I	C	herb	yes	3	yes	4	4	3	no
***Myosotis arvensis* Hill**	LC	L	7	I	B	herb	no	4	no	4	3	3	no
***Myosotis stricta* Roem. & Schult.**	LC		6	I	B	herb	yes	3	no	4	3	2	yes
***Myosoton aquaticum* (L.) Moench**	LC	L	1	I	B	herb	no	6	no	3	3	4	no
Neslia paniculata (*L.) Desv. *subsp. paniculata	VU	Z	7	I	C	herb	no	5	yes	3	4	3	yes
***Odontites vernus* (Bellardi) Dumort. *subsp. serotinus* Corb.**	VU	Z	5	I	B	herb	yes	8	no	4	4	1	no
Odontites vernus* (Bellardi) Dumort. *subsp. vernus	VU	Z	7	J	D	herb	yes	6	no	4	4	4	yes
***Ononis repens* L.**	LC	L	6	I	D	herb	no	6	no	4	3	2	no
***Ornithogalum umbellatum* L.**	LC	L	7	I	D	herb	no	4	yes	4	4	3	no

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***Oxalis fontana* Bunge**	LC		7	N	A	herb	no	6	yes	4	4	0	no
***Papaver argemone* L.**	VU	Z	7	A	C	herb	yes	4	yes	3	4	3	no
Papaver dubium* L. *subsp. dubium	LC	L	7	J	C	herb	yes	5	yes	3	4	3	no
***Papaver dubium* L. *subsp. lecoqii* (Lamotte) Syme**	LC	L	7	J	C	herb	yes	5	yes	3	4	3	no
***Papaver rhoeas* L.**	LC	L	7	A	C	herb	yes	5	yes	3	4	3	no
***Pastinaca sativa* L.**		L	8	J	B	herb	yes	5	no	4	4	3	no
***Petrorhagia prolifera (*L.) P. W. Ball & Heywood**	LC	L	6	I	C	herb	yes	6	yes	4	5	2	yes
***Phleum pratense* L.**	LC		8	J	B	grass	yes	6	no	4	3	4	no
***Phragmites australis* (Cav.) Steud.**	LC		4	I	B	grass	yes	7	no	3	3	3	no
***Picea abies* (L.) H. Karst.**	LC		1	I	D	herb	yes	5	no	1	2	3	no
***Picris hieracioides* L.**	LC		8	I	B	herb	yes	6	no	4	4	4	no
***Pimpinella major* (L.) Huds.**	LC	L	8	I	D	herb	yes	6	no	3	3	3	no
***Pisum sativum* L. *subsp. arvense* (L.) Asch. & Graebn.**	DD		7	A	C	legume	no	5	no	3	4	3	yes
***Plantago lanceolata* L.**	LC		8	I	B	herb	no	4	no	3	3	3	no
***Plantago major* L. *subsp. intermedia* (Gilib.) Lange**	LC		7	I	B	herb	no	6	no	4	4	3	no
Plantago major* L. *subsp. major	LC		7	I	B	herb	no	6	no	4	3	4	no
***Plantago media* L.**	LC	L	6	I	E	herb	no	5	no	4	3	2	no
***Poa alpina* L.**	LC		2	I	B	grass	yes	6	no	4	2	4	no
***Poa annua* L.**	LC		7	I	B	grass	yes	1	no	4	3	4	no
***Poa pratensis* L.**	LC		8	I	B	grass	no	5	no	4	3	3	no
***Poa trivialis* L.**	LC		8	I	B	grass	no	6	no	3	3	4	no
***Polygonum aviculare* L.**	LC		7	I	B	herb	no	5	no	4	3	4	yes
***Polygonum bistorta* L.**	LC	L	2	I	B	herb	no	5	no	3	3	4	no
***Polygonum hydropiper* L.**	LC	L	7	I	B	herb	no	7	no	3	3	4	no
Polygonum lapathifolium* L. *subsp. lapathifolium	LC		7	I	D	herb	no	7	no	5	3	4	yes

Species name	RL	UZL	Ecological group	Introduction	Spread	Life-form	Seed dispersal by wind	First month of flowering	Characteristic species	L	T	N	Annual
***Polygonum minus* Huds.**	LC		7	I	B	herb	no	7	no	3	4	4	no
***Polygonum mite* Schrank**	LC		7	I	D	herb	no	7	no	3	4	4	no
***Polygonum persicaria* L.**	LC		7	I	B	herb	no	7	yes	4	3	4	yes
Portulaca oleracea* L. *subsp. oleracea	LC		7	A	C	herb	no	6	yes	4	4	4	yes
***Potentilla anserina* L.**	LC		7	I	B	herb	no	5	no	4	3	4	no
***Potentilla reptans* L.**	LC		7	I	B	herb	no	6	no	4	3	4	no
***Prunella vulgaris* L.**	LC		8	I	B	herb	no	6	no	4	3	3	no
Ranunculus acris* L. *subsp. acris	LC		2	I	B	herb	yes	4	no	3	3	3	no
***Ranunculus acris* L. *subsp. friesianus* (Jord.) Syme**	LC		8	I	D	herb	yes	4	no	3	3	4	no
***Ranunculus arvensis* L.**	VU	Z	7	A	C	herb	no	5	yes	3	4	3	yes
***Ranunculus repens* L.**	LC		7	I	B	herb	yes	5	yes	3	3	4	no
***Ranunculus sardous* Crantz**	CR		7	I	C	herb	yes	5	no	4	4	3	yes
***Raphanus raphanistrum* L.**	LC		7	I	B	herb	no	5	yes	4	4	4	yes
***Rhinanthus alectorolophus* (Scop.) Pollich**	LC	L	5	I	D	herb	yes	5	no	4	3	3	yes
***Rhinanthus minor* L.**	LC	L	5	I	B	herb	yes	5	no	4	3	2	yes
***Rorippa islandica* (Gunnerus) Borbás**	NT	L	5	I	D	-	no	6	no	4	2	3	no
***Rorippa sylvestris* (L.) Besser**	LC	L	7	I	D	herb	yes	6	no	4	4	4	no
***Rubus caesius* L.**	LC		1	I	B	herb	no	6	no	2	4	4	no
***Rubus fruticosus* aggr.**	Lc		-	I	B	herb	no	5	no	3	4	4	no
***Rubus idaeus* L.**	LC		1	I	B	herb	no	5	no	3	3	4	no
***Rumex acetosa* L.**	LC		8	I	B	herb	yes	5	no	4	3	3	no
Rumex acetosella* L. *subsp. acetosella	LC		7	I	B	herb	yes	5	no	5	3	2	no
***Rumex crispus* L.**	LC		7	I	B	herb	yes	7	no	4	3	4	no
***Rumex obtusifolius* L.**	LC		8	I	D	herb	yes	6	no	4	3	4	no
***Sagina apetala* Ard.**	NT	L	7	I	C	herb	yes	5	no	4	3	1	no
***Sagina procumbens* L.**	LC		7	A	B	herb	yes	5	no	4	3	4	no

Species name	RL	UZL	Ecological group	Introduction	Spread	Life-form	Seed dispersal by wind	First month of flowering	Characteristic species	L	T	N	Annual
***Salvia pratensis* L.**	LC	L	6	I	C	herb	no	5	no	4	4	2	no
***Saponaria officinalis* L.**	LC	L	7	I	B	herb	yes	7	no	3	4	4	no
***Saxifraga tridactylites* L.**	LC	L	3	I	C	herb	yes	3	no	4	4	2	yes
***Scandix pecten-veneris* L.**	EN	Z	7	A	B	herb	no	5	yes	4	4	3	yes
Scleranthus annuus* L. *subsp. annuus	VU	Z	7	J	B	herb	yes	4	yes	4	4	2	no
***Secale cereale* L.**	LC		7	J	B	herb	no	5	no	5	3	3	no
***Securigera varia* (L.) Lassen**	LC	L	6	I	B	leguem	yes	6	no	3	4	2	no
***Sedum acre* L.**	LC	L	3	I	B	grass	yes	6	no	5	3	1	no
***Senecio vulgaris* L.**	LC		7	A	C	herb	yes	2	yes	4	4	4	no
***Setaria pumila* (Poir.) Roem. & Schult.**	LC		7	A	A	grass	no	7	yes	4	4	4	yes
***Setaria verticillata* (L.) P. Beauv.**	LC		7	A	A	grass	no	6	yes	4	5	4	yes
***Setaria viridis* (L.) P. Beauv.**	LC		7	A	C	grass	no	7	yes	4	4	4	yes
***Sherardia arvensis* L.**	LC	L	7	I	C	herb	no	5	yes	4	4	3	yes
***Silene dioica* (L.) Clairv.**	LC	L	8	I	D	herb	yes	4	no	3	3	4	no
***Silene noctiflora* L.**	VU	Z	7	A	B	herb	yes	6	yes	4	4	3	yes
***Silene pratensis* (Rafn) Godr.**	LC	L	7	I	B	herb	yes	5	no	4	4	4	no
Silene vulgaris* (Moench) Garcke *subsp. vulgaris	LC		6	I	D	herb	yes	6	no	3	3	2	no
***Sinapis arvensis* L.**	LC		7	A	C	herb	yes	5	yes	4	4	4	yes
***Sisymbrium officinale* (L.) Scop.**	LC	L	7	A	B	herb	yes	5	no	4	3	4	no
***Solanum nigrum* L.**	LC		7	I	B	herb	no	6	yes	4	4	4	yes
***Solanum tuberosum* L.**	LC		7	J	A	herb	no	6	no	4	4	4	no
***Solidago canadensis* L.**	LC		7	N	A	herb	yes	8	no	3	4	3	no
Sonchus arvensis* L. *subsp. arvensis	LC		7	I	B	herb	yes	7	yes	3	4	4	no
***Sonchus asper* Hill**	LC		7	I	B	herb	yes	6	yes	4	4	4	no
***Sonchus oleraceus* L.**	LC		7	J	B	herb	yes	6	yes	4	4	4	no
***Spergula arvensis* L.**	VU	Z	7	I	C	herb	yes	6	no	3	3	3	yes
***Spergularia rubra (*L.) J. & C. Presl**	LC		7	A	B	herb	yes	5	no	4	3	3	no

Species name	RL	UZL	Ecological group	Introduction	Spread	Life-form	Seed dispersal by wind	First month of flowering	Characteristic species	L	T	N	Annual
***Spergularia segetalis* (L.) Don**	RE		7	I	D	herb	yes	5	no	4	4	3	yes
***Stachys annua* (L.) L.**	VU	Z	7	A	C	herb	no	6	yes	4	4	2	yes
***Stachys palustris* L.**	NT	L	5	I	B	herb	no	6	no	3	4	3	no
***Stellaria graminea* L.**	LC		8	I	B	herb	yes	5	no	3	3	3	no
***Stellaria media* (L.) Vill.**	LC		7	I	C	herb	yes	3	yes	3	3	4	no
***Symphytum officinale* L.**	LC	L	5	I	B	herb	no	5	no	3	4	4	no
***Taraxacum officinale* aggr.**	LC		8	I	B	herb	yes	4	no	4	3	4	no
***Teucrium botrys* L.**	NT	L	7	I	D	herb	yes	6	no	4	4	2	no
***Thlaspi arvense* L.**	LC		7	A	B	herb	yes	4	yes	3	3	4	no
***Thlaspi perfoliatum* L.**	LC		6	I	B	herb	yes	4	no	4	4	3	no
***Tragopogon pratensis* L. *subsp. orientalis* (L.) Celak.**	LC	L	8	I	B	herb	yes	5	o	4	4	3	no
***Trifolium arvense* L.**	LC	L	7	I	C	legume	yes	5	yes	4	4	1	no
***Trifolium campestre* Schreb.**	LC	L	7	A	C	legume	yes	5	no	4	4	2	no
***Trifolium incarnatum* L.**	LC		8	I	C	legume	yes	5	no	5	4	0	no
Trifolium pratense* L. *subsp. pratense	LC		8	I	B	legume	yes	5	no	3	3	3	no
***Trifolium repens* L.**	LC		8	I	B	legume	yes	5	no	3	4	0	no
***Tripleurospermum perforatum* (Mérat) Laínz**	LC		7	A	B	herb	yes	6	no	4	4	4	no
***Trisetum flavescens* (L.) P. Beauv.**	LC		-	I	B	grass	yes	5	no	4	3	4	no
***Triticum aestivum* L.**	LC		7	J	C	grass	no	6	no	5	4	4	no
***Tussilago farfara* L.**	LC		3	I	B	herb	yes	3	no	4	3	3	no
***Urtica dioica* L.**	LC		7	I	B	herb	yes	6	no	3	3	5	no
***Valerianella dentata* (L.) Pollich**	VU	Z	7	A	C	herb	yes	4	yes	4	4	4	yes
***Valerianella locusta* (L.) Laterr.**	LC	L	7	I	C	herb	yes	3	yes	4	4	4	no
***Valerianella rimosa* T. Bastard**	EN	Z	7	A	C	herb	yes	5	yes	4	4	4	yes
Verbascum thapsus* L. *subsp. thapsus	LC		7	I	B	herb	no	6	no	5	4	4	no

Species name	RL	UZL	Ecological group	Introduction	Spread	Life-form	Seed dispersal by wind	First month of flowering	Characteristic species	L	T	N	Annual
***Veronica agrestis* L.**	LC	L	7	A	B	herb	no	3	yes	4	4	4	yes
***Veronica arvensis* L.**	LC	L	7	I	C	herb	no	4	yes	3	4	4	yes
***Veronica chamaedrys* L.**	LC		8	I	B	herb	yes	4	no	3	3	4	no
***Veronica filiformis* Sm.**	LC		8	N	E	herb	no	4	no	4	4	3	no
Veronica hederifolia* L. *subsp. hederifolia	LC		7	I	B	herb	no	3	yes	3	4	4	no
***Veronica persica* Poir.**	LC		7	N	A	herb	no	2	yes	4	4	4	no
***Veronica polita* Fr.**	LC	L	7	A	C	herb	no	3	yes	4	4	4	yes
***Veronica serpyllifolia* L.**	LC		7	I	B	herb	no	5	no	4	4	4	no
***Veronica triphyllos* L.**	VU	Z	7	I	C	herb	yes	3	yes	4	4	3	yes
Vicia cracca* L. *subsp. cracca	LC	L	8	I	B	legume	no	6	no	4	3	3	no
***Vicia cracca* L. *subsp. incana* (Gouan) Rouy**	LC		7	I	D	legume	no	6	no	3	4	3	no
***Vicia faba* L.**	LC		7	J	C	legume	no	6	no	3	4	4	yes
***Vicia hirsuta* (L.) Gray**	LC		7	A	C	legume	no	5	yes	4	3	2	yes
***Vicia sativa* L.**	LC		7	I	C	legume	no	5	no	4.5	3	0	no
***Vicia sativa* L. *subsp. nigra* (L.) Ehrh.**	LC		7	I	C	legume	no	5	yes	4.5	3	0	no
Vicia sativa* L. *subsp. sativa	LC		7	J	C	legume	no	6	no	3	5	3	no
***Vicia sepium* L.**	LC		8	I	B	legume	no	4	no	3	3	0	no
***Vicia tetrasperma* (L.) Schreb.**	NT		7	A	B	legume	no	5	yes	3	4	2	yes
***Vicia villosa* Roth**			7	I	C	legume	no	6	yes	3	4.5	3	no
***Viola arvensis* Murray**	LC		7	A	C	herb	no	3	yes	3	3	3	no

Appendix B: Table of arable weed species with high change in frequency between historical and contemporary plots.

Species	Historical frequency [%]	Contemporary frequency [%]	Change in frequency [%]
***Brassica napus* L.**	0.43	4.74	1000
***Echinochloa crus-galli* (L.) P. Beauv.**	2.59	16.81	550
***Amaranthus retroflexus* L.**	1.72	8.19	375
***Lolium multiflorum* Lam.**	4.31	20.26	370
***Ranunculus acris* L. *subsp. friesianus* (Jord.) Syme**	0.86	3.88	350
***Lolium perenne* L.**	5.60	21.12	277
***Pimpinella major* (L.) Huds.**	0.43	1.29	200
***Dactylis glomerata* L.**	3.45	9.48	175
***Solanum tuberosum* L.**	1.72	4.74	175
***Adonis aestivalis* L.**	1.72	3.45	100
***Festuca pratensis* Huds.**	0.86	1.72	100
***Geranium molle* L.**	0.86	1.72	100
***Lactuca serriola* L.**	0.43	0.86	100
***Galinsoga ciliata (*Raf.) S. F. Blake**	0.00	4.31	-
***Agropyron intermedium* (Host) P. Beauv.**	0.00	3.02	-
***Triticum aestivum* L.**	0.00	3.02	-
***Secale cereale* L.**	0.00	2.59	-
***Avena sativa* L.**	0.00	2.16	-
***Geranium pyrenaicum* Burm. f.**	0.00	1.72	-
***Rorippa sylvestris (*L.) Besser**	0.00	1.72	-
***Trifolium pratense* L.**	12.93	5.17	-60
***Daucus carota* L.**	6.47	2.59	-60
***Oxalis fontana* Bunge**	5.60	2.16	-61.54
***Chenopodium polyspermum* L.**	25.00	9.48	-62
***Veronica hederifolia* L.**	6.90	2.59	-62.5
***Fallopia convolvulus* (L.) Á. Löve**	61.64	22.84	-63
***Buglossoides arvensis* (L.) I. M. Johnst.**	8.19	3.02	-63
***Galium mollugo* aggr.**	3.88	1.29	-66.5
***Anchusa arvensis* (L.) M. Bieb.**	2.59	0.86	-66.5
***Tripleurospermum perforatum (*Mérat) Laínz**	2.59	0.86	-66.5
***Bunium bulbocastanum* L.**	1.29	0.43	-66.5
***Bupleurum rotundifolium* L.**	1.29	0.43	-66.5
***Lotus corniculatus* L.**	1.29	0.43	-66.5
***Papaver dubium* L. *subsp. lecoqii* (Lamotte) Syme**	1.29	0.43	-66.5
***Urtica dioica* L.**	1.29	0.43	-66.5
***Polygonum persicaria* L.**	44.40	14.66	-67
***Sonchus arvensis* L.**	18.97	6.03	-68
***Lapsana communis* L.**	16.38	5.17	-68.5
***Viola arvensis* Murray**	56.03	17.24	-69
***Convolvulus arvensis* L.**	47.41	14.22	-70
***Matricaria recutita* L.**	12.93	3.88	-70
***Capsella bursa-pastoris (*L.) Medik.**	41.81	12.50	-70
Vicia cracca* L. *subsp. cracca	16.38	4.74	-71
***Aethusa cynapium* L.**	22.41	6.47	-71
***Glechoma hederacea* L.**	6.03	1.72	-71.5
***Potentilla anserina* L.**	4.74	1.29	-72.5
***Galeopsis tetrahit* L.**	50.86	13.36	-73.56
***Galium aparine* L.**	46.55	12.07	-74
***Veronica arvensis* L.**	18.53	4.74	-74.5
***Papaver rhoeas* L.**	31.03	7.76	-75
***Rumex obtusifolius* L.**	24.14	6.03	-75
***Senecio vulgaris* L.**	10.34	2.59	-75
***Anthriscus sylvestris* (L.) Hoffm.**	3.45	0.86	-75
***Agrostis capillaris* L.**	1.72	0.43	-75
***Carum carvi* L.**	1.72	0.43	-75

Species	Historical frequency [%]	Contemporary frequency [%]	Change in frequency [%]
***Melampyrum arvense* L.**	1.72	0.43	-75
***Cirsium arvense* (L.) Scop.**	38.36	9.05	-76.5
***Potentilla reptans* L.**	5.60	1.29	-77
***Alchemilla vulgaris* aggr.**	3.88	0.86	-78
***Setaria viridis* (L.) P. Beauv.**	3.88	0.86	-78
***Mercurialis annua* L.**	6.03	1.29	-78.5
***Heracleum sphondylium* L.**	12.50	2.59	-79
***Ranunculus arvensis* L.**	8.62	1.72	-80
***Bromus hordeaceus* L.**	2.16	0.43	-80
***Euphorbia platyphyllos* L.**	2.16	0.43	-80
***Galeopsis angustifolia* Hoffm.**	2.16	0.43	-80
***Veronica serpyllifolia* L.**	2.16	0.43	-80
***Achillea millefolium* aggr.**	31.03	6.03	-80.5
***Equisetum arvense* L.**	26.72	5.17	-80.5
***Medicago lupulina* L.**	6.90	1.29	-81.25
***Rumex crispus* L.**	11.64	2.16	-81.5
***Sonchus oleraceus* L.**	19.40	3.45	-82
***Ranunculus repens* L.**	57.33	9.91	-82.5
***Apera spica-venti (*L.) P. Beauv.**	25.43	4.31	-83
***Kickxia elatine* (L.) Dumort.**	2.59	0.43	-83.5
***Stachys palustris* L.**	2.59	0.43	-83.5
***Veronica agrestis* L.**	2.59	0.43	-83.5
Fumaria officinalis* L. *subsp. officinalis	5.60	0.86	-84.5
***Campanula rapunculoides* L.**	8.62	1.29	-85
***Kickxia spuria* (L.) Dumort.**	9.05	1.29	-85.5
***Spergula arvensis* L.**	6.03	0.86	-85.5
***Arrhenatherum elatius* (L.) J. & C. Presl**	3.02	0.43	-85.5
***Rhinanthus alectorolophus* (Scop.) Pollich**	3.02	0.43	-85.5
***Sinapis arvensis* L.**	34.91	4.74	-86.5
***Silene noctiflora* L.**	9.91	1.29	-87
***Cerastium fontanum* Baumg. *subsp. vulgare* (Hartm.) Greuter & Burdet**	23.28	3.02	-87
***Arenaria serpyllifolia* L.**	20.69	2.59	-87.5
***Galium spurium* L.**	3.45	0.43	-87.5
***Holcus lanatus* L.**	3.45	0.43	-87.5
***Hypericum humifusum* L.**	3.45	0.43	-87.5
***Lamium amplexicaule* L.**	3.45	0.43	-87.5
***Symphytum officinale* L.**	3.45	0.43	-87.5
***Myosotis arvensis* Hill**	56.90	6.90	-88
***Sonchus asper* Hill**	34.48	3.88	-88.75
***Rumex acetosa* L.**	4.31	0.43	-90
***Raphanus raphanistrum* L.**	25.43	2.16	-91.5
***Atriplex patula* L.**	25.86	2.16	-91.5
***Riccia glauca* L.**	5.17	0.43	-91.5
***Tussilago farfara* L.**	5.17	0.43	-91.5
***Vicia sepium* L.**	5.17	0.43	-91.5
***Lathyrus pratensis* L.**	11.21	0.86	-92.5
***Vicia tetrasperma* (L.) Schreb.**	12.07	0.86	-93
***Anagallis arvensis* L.**	37.93	2.59	-93
***Agrostemma githago* L.**	6.47	0.43	-93.5
***Legousia speculum-veneris* (L.) Chaix**	6.47	0.43	-93.53
***Valerianella locusta* (L.) Laterr.**	8.19	0.43	-94.5
***Agrostis stolonifera* L.**	25.43	1.29	-95
***Aegopodium podagraria* L.**	8.62	0.43	-95
***Chaenorrhinum minus* (L.) Lange**	9.48	0.43	-95.5
***Sherardia arvensis* L.**	11.64	0.43	-96.5
***Cerastium glomeratum* Thuill.**	12.07	0.43	-96.5
***Vicia sativa* L. *subsp. nigra (*L.) Ehrh.**	14.22	0.43	-97
***Prunella vulgaris* L.**	14.66	0.43	-97
***Aphanes arvensis* L.**	15.95	0.43	-97.5
***Euphorbia exigua* L.**	20.26	0.43	-98

Species	Historical frequency [%]	Contemporary frequency [%]	Change in frequency [%]
***Mentha arvensis* L.**	23.71	0.43	-98
***Vicia hirsuta* (L.) Gray**	25.86	0.43	-98.5
***Chrysanthemum leucanthemum* L.**	15.95	0.00	-100
***Sagina procumbens* L.**	15.52	0.00	-100
Vicia sativa* L. *subsp. sativa	12.50	0.00	-100
***Plantago major* L. *subsp. intermedia* (Gilib.) Lange**	12.07	0.00	-100
***Gnaphalium uliginosum* L.**	10.34	0.00	-100
***Holcus mollis* L.**	10.34	0.00	-100
***Polygonum mite* Schrank**	9.48	0.00	-100
***Arabidopsis thaliana* (L.) Heynh.**	8.62	0.00	-100
***Juncus bufonius* L.**	8.19	0.00	-100
***Knautia arvensis (*L.) Coult.**	7.33	0.00	-100
Ranunculus acris* L. *subsp. acris	6.03	0.00	-100
***Anagallis foemina* Mill.**	5.60	0.00	-100
***Stellaria graminea* L.**	5.60	0.00	-100
***Papaver dubium* L.**	5.17	0.00	-100
Centaurea scabiosa* L. *subsp. scabiosa	3.88	0.00	-100
***Linaria vulgaris* Mill.**	3.88	0.00	-100
***Picris hieracioides* L.**	3.88	0.00	-100
***Scleranthus annuus* L.**	3.88	0.00	-100
***Veronica chamaedrys* L.**	3.88	0.00	-100
***Euphorbia peplus* L.**	3.02	0.00	-100
***Rumex acetosella* L.**	3.02	0.00	-100
Odontites vernus (*Bellardi) Dumort. *subsp. serotinus Corb.	2.59	0.00	-100
***Anthoceros* spec.**	2.16	0.00	-100
***Chaerophyllum aureum* L.**	2.16	0.00	-100
***Chaerophyllum hirsutum* L.**	2.16	0.00	-100
***Papaver argemone* L.**	2.16	0.00	-100
***Trifolium campestre* Schreb.**	2.16	0.00	-100
***Valerianella dentata* (L.) Pollich**	2.16	0.00	-100
***Valerianella rimosa* T. Bastard**	2.16	0.00	-100
***Veronica polita* Fr.**	2.16	0.00	-100
***Vicia sativa* L.**	2.16	0.00	-100
***Acinos arvensis* (Lam.) Dandy**	1.72	0.00	-100
***Crepis capillaris* Wallr.**	1.72	0.00	-100
***Erysimum cheiranthoides* L.**	1.72	0.00	-100
***Galeopsis ladanum* L.**	1.72	0.00	-100
***Gypsophila muralis* L.**	1.72	0.00	-100
***Lysimachia nummularia* L.**	1.72	0.00	-100
***Myosoton aquaticum* (L.) Moench**	1.72	0.00	-100

Chapter III

The Assembly of Agricultural Plant Communities in Switzerland

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Abstract

Aim

We explore the factors controlling the assembly of arable weed communities and of intensely used meadow communities. In particular, we test whether filtering by the stringent environmental conditions of agriculture or competition among the species of a large pool of species structured the weed and meadow communities and whether the relative importance of these two processes changed during the recent past due to changed agricultural practices.

Location

Switzerland (CH)

Methods

We used two sets of vegetation relevés from across Switzerland with abundance estimates of the constituent plant species. One set contains 232 historical relevés of arable fields and 232 matching contemporary relevés that were recorded from the same location with the same crop type as the historical relevés. The other set contained 232 historical relevés of intensively used meadows and 232 contemporary relevés of meadows, although not from the same locations. We explored the phylogenetic structure of these four communities using phylogenetic community assembly analysis, and assessed the change in diversity and composition of plant functional traits from historical to contemporary communities .

Results

Species and family richness decreased by about 25% from historical to contemporary samples in both sets of agricultural relevés. We found that phylogenetic clustering increased from traditionally managed to contemporary agricultural habitats. Furthermore, there was a general increase in phylogenetic clustering from meadows to arable habitats. These patterns were accompanied by a decrease in the diversity, and a change in the composition of plant functional traits.

Main conclusions

The intensification of agricultural practices led to a higher degree of environmental filtering in both meadows and arable fields. The loss of phylogenetic and trait variation as well as in species richness could reduce the resilience of communities and their ability to adapt to environmental changes.

Keywords: agricultural landscape, arable flora, community assembly, conservation, disturbance, functional traits, grassland, homogenization, phylogeny, species loss

Introduction

The processes regulating the assembly of plant communities have received much attention (Webb, 2000a; Cavender-Bares *et al.*, 2004; Silvertown *et al.*, 2006; Whitfeld *et al.*, 2012). Early studies invoked limiting ecological similarity among species as an important community assembly criterion (MacArthur & Levins, 1967; Weiher *et al.*, 1998; Wilson, 2007). However, more recently, the focus has shifted to a duality of processes: filtering (only those species with a specific set of traits can survive) and competition (allowing only species with a particular set of traits to survive). Theory predicts that filtering should be more common in communities exposed to intense selection, while competition should predominate in more mesic environments (Tofts & Silvertown, 2000). In communities which have been stable for a long time and where environmental conditions are not too severe, diverse species can survive, and the community is primarily structured by competition (Leibold, 1998). In contrast, habitats which are often disturbed or exposed to other harsh environmental conditions, only well adapted species can survive as the community is primarily structured by filtering (Booth & Swanton, 2002).

The development of phylogenetic community analyses (Webb, 2000a) has provided the field of community assembly with a major new stimulus. This has been fostered by the development of molecular methods which allow the inference phylogenetic trees down to low taxonomical levels. These analyses shed light on the phylogenetic structure of communities and consequently the processes that form the communities (Pavoine & Bonsall, 2011). If competition between the species controls their assembly, then they should be phylogenetically over-dispersed. Over dispersion means that the constituent species are less closely related to each other than expected if they were assembled randomly. On the other hand, if environmental stress or habitat filtering (e.g. through generalist enemies) controlled species assembly, then phylogenetic clustering (where constituent species are more closely related than randomly expected) is predicted (Cavender-Bares *et al.*, 2009).

In clustered or overdispersed communities, co-occurring species are thus more closely or more distantly related to each other than in a randomly chosen community, respectively (Emerson & Gillespie, 2008). Analysing phylogenetic structure therefore gives insight into the underlying ecological processes that formed communities (Webb, 2000b).

Most studies on phylogenetic effects on species assembly deal with communities in more or less undisturbed or stable habitats or in habitats along a natural successional gradient (Cavender-Bares *et al.*, 2006; Emerson & Gillespie, 2008; Kluge & Kessler, 2011). Only few studies have been conducted on communities of disturbed habitats or on short-lived communities (Webb *et al.*, 2002; Knapp *et al.*, 2010). However, no studies on phylogenetic effects on species assembly comparing communities of meadows and weeds of arable fields (hereafter "weeds") have - to our knowledge - been conducted so far. Still, over 15 million km^2 (about 10%) of the terrestrial surface of the earth is used for crop production, and another 34 million km^2 of the earth's surface (about 24%) is covered with meadows or pastures (Klein Goldewijk *et al.*, 2007). As arable fields are a man-made habitat that is regularly disturbed, we postulate that environmental stress is the dominant driving force for community composition and hence predict that weed communities in arable fields should show phylogenetic clustering. We chose meadow communities for comparison with weed communities as they also represent agricultural habitats, but are more stable than arable fields as anthropogenic management has – even if regular - a less profound impact on the current species than in arable fields (Silvertown *et al.*, 2001). A study that compared undisturbed with recently disturbed arable fields indeed found phylogenetic clustering in disturbed habitats while undisturbed communities showed no phylogenetic pattern (Dinnage, 2009). Similarly, Knapp *et al.* (2008) found more phylogenetic clustering in highly disturbed urban habitats than in rural habitats. Hence, we hypothesize that man-made stress increases from traditionally harvested meadows over modern, intensively managed meadows to arable fields and that phylogenetic clustering should thus increase in the same order.

The existence of a vegetation database with over 23'000 georeferenced relevés from Switzerland taken between 1886 and 2013 provides the opportunity to explore changes in phylogenetic patterns and composition of agricultural plant communities. We selected historical and contemporary relevés from weed communities from arable fields and from meadows to test the following hypotheses. Firstly, that contemporary communities in both arable fields and meadows would be more phylogenetically clustered than historical communities, possibly due to an increase in disturbance and stress. Secondly, for the same reason, weed communities will be more clustered than meadows. In addition, we expected that trait composition changes from historical to contemporary relevés as well as from weed to meadow communities, reflecting these changes in the disturbance regime. We thus test for the factors that control the assembly of agricultural species as well as the functional trait composition of agricultural communities.

Methods

The historical relevés were taken from all parts of Switzerland and species richness per plot was recorded using the Braun-Blanquet scale (Braun-Blanquet, 1928). The plant names were standardized to the taxonomy used in InfoFlora (InfoFlora, 2014). Of these datasets over 13'000 relevés were taken of grassland and over 4500 on arable fields. The first meadow relevés were recorded in 1886 and arable field relevés in 1927.

Floristic data

For the contemporary floristic data different approaches for weed and for meadow relevés were used. For the dataset of arable fields, we picked a stratified random sample of the over 4'500 pre-1980 relevés. The strata consisted of biogeographic region (Jura (JU), Midlands (ML), northern Alps (NA), southern Alps (SA), eastern central Alps (EZA) and western central Alps (WZA, Gonseth *et al.*, 2001)), recorder, Red List status and crop type (wheat, barley, beet or potato). We first filtered out those locations at which the contemporary and historical crop-types differed. We then repeated 232

vegetation relevés of rectangular plots of 100m^2 at the same location as the historical relevés in 2012 and 2013 (N. Richner, submitted). The plots were placed at least 3m from field margins, to minimise the influence of field borders. We recorded only presence (not abundance) of non-crop species. The study sites were distributed between 245m and 1670m above sea level. .

For the meadow dataset, we selected the same altitudinal range as the relevés for arable fields. Subsequently, a stratified random sample was taken with biogeographic region (see above) and time period as strata. The two time periods contained either historical (before 1980) or contemporary (after 1980) relevés, respectively. For each time period, we then selected 232 relevés of 25 m^2 size. Note that, in contrast to the arable field relevés, historical and contemporary meadow relevés were not carried out at the same location.

Analysis of phylogenetic structure

The phylogenetic trees were assembled using the online tool PHYLOMATIC (Webb & Donoghue, 2005). A list of all species with relevant family and genus was imported into PHYLOMATIC and separate supertrees were constructed for weed and meadow species, using the pooled taxa of all included relevés in the relevant habitat. The structure of the data was analysed with PHYLOCOM using the supertrees and sample data of the vegetation relevés (Webb *et al.*, 2008). We compared the samples using the net relatedness index (NRI) and the nearest taxon index (NTI) compiled by PHYLOCOM. NRI is a measure for the mean phylogenetic distance (MPD) between the random community – which was built using the null-model where the species of a sample were random drawn from the whole species pool of the relevant habitat - and the observed community. Highly positive values point to a phylogenetically clustered community, while low or negative values indicate that the species in the community are evenly spread or overdispersed across the phylogenetic tree. MPD is the sum of all pairwise distances among all pairs of species in the community. NTI measures the extent of terminal clustering on the phylogeny. It is calculated using

the mean net relatedness distance (MNRD) which measured the minimal distance or branch length between taxa in a particular community. As in NRI, highly positive values of these indices indicate clustering of taxa, while low or negative values indicate overdispersion of taxa across the phylogeny. We removed relevés with fewer than two species, because no distances could be calculated for these relevés (n=23).

$$NRI_{\text{sample}} = -1 * \frac{MPD_{\text{sample}} - MPD_{\text{rmdsample}}}{sd(MPD_{\text{rmdsample}})} \quad (1)$$

$$NTI_{\text{sample}} = -1 * \frac{MNRD_{\text{sample}} - MNTD_{\text{rmdsample}}}{sd(MNTD_{\text{rmdsample}})} \quad (2)$$

The null-model was built by randomly assembling communities from the whole species pool recorded from the relevant habitat (999 permutations) maintaining the species richness of each sample. A community was defined as all plant species growing in a plot of 100m^2 for weed communities and for 25m^2 for meadow communities. To test if the average phylogenetic signal between historical and contemporary surveys differed we used two-sided Wilcoxon-tests (Cooper *et al.*, 2008).

Functional trait data

We used the following functional traits for all species in arable fields and meadows: growth form (herbs, grasses, legumes), life-history (type of seed dispersal: wind dispersed or not wind-dispersed, beginning and duration of flowering, seed longevity, r-, c- or s-strategy (Grime, 1977), ecological group (forest plant, wetland plant, unfertilized dry meadow plant, fertilized meadow plant, weeds and ruderals, pioneers, other plants), time of introduction to Europe (idiochrophyte: native or naturally immigrated species; archaeophyte: introduced before AD 1500; neophyte: introduced after AD 1500) and indicator values for light, nutrients and temperature. The indicator values are dimensionless, meristic values between 1 and 5. High values mean a high affinity of the species for high light availability, nutrient rich soils and high temperatures, respectively. The functional traits

were scored based on the Flora Indicativa (Landolt *et al.*, 2010). Traits for all recorded species are listed in Appendix A.

Analysis of functional traits

We inferred generalised linear models (GLM) to explain the variation in NRI and NTI values in terms of functional traits. The models were ranked based on the Akaike information criterion (AIC) and their significance assessed using likelihood-ratio tests (Venables & Ripley, 2002).

Differences in the trait composition among communities and between historical and current communities were explored with a principal component analysis (PCA) of trait distribution on the relevé level. Categorical traits values were included as present or absent in a species.

To calculate changes in the diversity of traits among the communities, we used the Shannon-Wiener index (H'). The index is calculated as follows, using the number and distribution of traits per relevé:

$$H' = -\sum_{i=1}^{S} p * \ln(p) \quad (3)$$

with

$$p = \frac{n}{N} \quad (4)$$

Where s denotes the total number of traits, N the sum of the values of all present traits, n the value of trait i and p the value of each trait.

Results

General phylogenetic assembly

We found the greatest richness of species, genera and families in historical meadows. These numbers decreased from historical over contemporary meadows to historical weed communities and contemporary weed communities (Table 1). The total number of species for the whole meadow

dataset with 9500 relevés declined by about 20%. The percentage of losses in species, genera and families of meadows and weed communities did not differ ($p > 0.6$). Comparing historical to contemporary meadows, six families were lost and two families were gained. In weed communities, eight families were lost and two gained. Most families did not change in their percentage of total number of species. However, we observed an increase of *Poaceae* and a decrease of *Caryophyllaceae* from historical to contemporary weed relevés (Table 2). For the combined weed relevés, NRI and NTI values were higher than for the combined meadow relevés ($p_{two\text{-}tailed} < 0.001$;Table 3). MPD significantly declined from meadow to weed relevés from 16.23 to 13.18 ($p < 0.001$) and both communities had values significantly smaller than for the null-model (14.43; $p < .001$ in both cases).

Historical vs. contemporary relevés

For weed relevés, NTI increased significantly from 0.35 in historical relevés to 0.75 in contemporary relevés ($p_{two\text{-}tailed} < 0.001$), while NRI did not change (Table 4; Fig. 2c, d). In meadow relevés, NRI and NTI increased from historical to contemporary relevés significantly from 0.43 to 0.16 and 1.06 to 1.29, respectively ($p_{two\text{-}tailed} < 0.001$ and $p_{two\text{-}tailed} < 0.05$, respectively; Table 4). There was no difference in NRI or NTI between weed communities in cereals (wheat, barley, spelt and rye) or root crops (sugar-beet and potatoes; Fig. 1). Historical as well as contemporary weed communities were more phylogenetically clustered than historical or contemporary meadow communities with respect to both NRI and NTI values ($p_{two\text{-}tailed} < 0.001$; Table 3, Fig. 2c, d). We found a positive correlation between phylogenetic clustering and habitat disturbance (Fig. 2). MPD of meadow relevés declined from 16.45 (± 0.8 SE) to 15.98 (± 0.8; $p_{two\text{-}tailed} < 0.001$). MPD of historical meadow relevés was significantly larger than the null-model, while MPD of contemporary meadow relevés was significantly smaller than expected ($p_{two\text{-}tailed} < 0.001$). From historical to contemporary weed relevés, MPD declined from 13.66 to 12.62 ($p_{two\text{-}tailed} < 0.001$). MPD of historical and contemporary weed relevés was significantly smaller than the null-model ($p_{two\text{-}tailed} < 0.001$).

Mean species number declined from historical to contemporary relevés in weed as well as in meadow relevés (Fig. 2a). While species had a slightly higher extinction risk if there were no other species from the same genus present, there is currently a higher percentage of locally monotypic genera (27.4%) than in the historical relevés (25.1%). However, there was no significant phylogenetic pattern in species lost or gained across time.

Change in trait composition

The Shannon index of traits for weed relevés decreased significantly with increased clustering in contemporary weed communities; contemporary weed communities had the smallest Shannon-Index and the highest level of phylogenetic clustering. Meadow communities showed no such trend. The PCA of trait-distribution per relevé showed a clear separation of historical and contemporary weed relevés while for meadows no clear pattern was observed (Fig. 3). The main factors influencing the distribution of relevés were the percentage of archeophytes, species with high seed longevity, annuals, grasses and fertilized meadow plants.

Phylogenetic clustering (NTI as well as NRI) for historical relevés was negatively correlated with the mean indicator value for nutrients, while this indicator value increased for contemporary relevés of combined weed and meadow communities (Fig. 4). NRI and NTI were positively correlated with the indicator value for humidity, annual life history and the percentage of plants flowering for one or three months and was negatively correlated with the percentage of herbs and legumes per relevé (Table 5). Phylogenetic clustering (NRI) was negatively correlated with the length of the flowering period per community. While r-strategists constituted a higher percentage of the flora in phylogenetically clustered communities, the c- and s-strategists reached higher percentages in less clustered communities.

Discussion

We found that for both weed and meadow communities the total number of species as well as the richness in families declined by about 20% and 25%, respectively, across Switzerland in the last 100 years. In contemporary weed communities, phylogenetic clustering was higher than in historical communities (based on NTI, but not NRI). In contemporary meadows, on the other hand, phylogenetic clustering was also higher than in historical meadows (based on both NTI and NRI). Overall, weed communities were, however, more phylogenetically clustered than meadow communities. With increasing phylogenetic clustering, a decrease in trait diversity in both meadow and weed communities was found. The trait profile in weed communities, but not in meadows, changed from historical to contemporary weed communities.

Changes in phylogenetic structuring

We found a 21% loss of species and 25% of family richness from historic to contemporary relevés. There are surprisingly few comparable studies from Switzerland. No change in species number was detected in several studies on mountain hay-meadows (Fischer & Stöcklin, 1997; Homburger & Hofer, 2012), but these studies only covered changes since 1960, and the biggest losses may have happened before 1960 (Walter *et al.*, 2010). However, Fischer and Stöcklin (1997) as well as Homburger and Hofer (2012) found that characteristic species of these habitats declined or vanished and were replaced by new and often generalist species. During the last ten years, species richness did not change in any habitat of Switzerland according to the Swiss biodiversity monitoring program (BDM, 2013). Habitats in urban landscapes even showed an increase in total species number due to neophytes. However, our longer-term results for meadow communities are corroborated by a comparison of over 9500 relevés of meadows from the vegetation database which showed a decrease of about 20% in species number from historical to contemporary relevés. The fact that species richness in different habitats did not change in the last ten years could indicate that the loss

in species richness may have been halted. However, especially in the agricultural habitats of the lowlands, species richness was already at a very low level. Therefore, rates of change may have slowed down.

The percentages of the most frequent families in historical arable fields were comparable to those found by Holzner and Numata (1982) for weed communities across Europe. Some families lost more species than others, but there was no significant difference for lost species to belong to species poor families; a result in line with Fried et al. (2009). However, a family with only one species is lost with its last remaining species, consequently this particular species loss has more phylogenetic impact than species loss in more species-rich families. The taxonomic pattern of species loss was the same in weed and meadow communities, even though they experienced a different set of constraints over the past century. This is surprising, as with increasing globalisation, more and more neophytes are reported in Switzerland and many of these are ruderal plants also living in arable fields (Landolt *et al.*, 2010). It was hence no surprise that we found a higher percentage of neophytes in contemporary than in historical relevés in this study. Still, as the total species richness in the highly disturbed habitat of arable fields decreased, we assume that the loss of indigenous plant species and families was even more pronounced than in the semi-natural communities such as meadows, as species losses were compensated by the introduction of neophytes.

What caused the loss of species in agricultural communities? Based on the increased phylogenetic clustering from historical to contemporary communities and between meadows to arable fields we suggest that the losses were due to increased environmental filtering (Webb, 2000a; Kraft *et al.*, 2007). Habitat filtering is the result of strong selective environmental factors, allowing only species with the necessary adaptations to survive. As these adaptations might have evolved only a few times, it is most parsimonious to assume that these adaptations were inherited from a common ancestor and that the bearers are thus phylogenetically related. This explanation is in

accordance with studies from various habitat-types that found filtering as the main cause for phylogenetic clustering (Helmus *et al.*, 2007; Emerson & Gillespie, 2008). At larger spatial scales environmental filtering has greater impact on community assembly than competition among species (Cavender-Bares *et al.*, 2006). Therefore, one could argue that our results for meadow and arable field communities across Switzerland are not surprising. However, we compared two different systems with the same spatial distribution. As the spatial component of filtering affects both communities to the same extent, the comparison of the two systems is not influenced by spatial scale. Therefore, the spatial component of filtering effect is negligible as we did not look at the processes influencing a single community.

In meadow habitats, the filter may have consisted mainly of increased fertilizer levels (Zechmeister *et al.*, 2003; Peter *et al.*, 2008) and more frequent mowing, but also the fact that in meadows the use of seed-mixtures to improve fodder quality increased (Robinson & Sutherland, 2002; Vuckovic *et al.*, 2005). Unfortunately, no information was given with the relevés on whether and which meadow seed-mixtures were used or not. NRI and NTI values showed the same pattern of increase from historical to contemporary relevés. In the case of arable habitats, there generally was a higher mechanisation of agricultural management (e.g. higher disturbance through tyres), change in sowing season of the crop, and an increased input of industrial fertilizer and herbicides (Robinson & Sutherland, 2002; Herzog *et al.*, 2006). The higher fertilizer input resulted in a shift in species composition to higher nutrient status filtering against species with low nutrient requirements. The input of herbicides filtered for species tolerant or resistant against herbicides. The increase of traffic on the fields due to herbicide and fertilizer application increased the mechanical damage to soil from the tyre pressure. Therefore, current arable habitats have a higher level of disturbance which results in increased filtering. The increasing clustering of arable compared to meadow communities could therefore be explained as the result of higher impact of disturbance on plant species due to tilling

and herbicide application (Dinnage, 2009). Knapp *et al.* (2008) found more phylogenetic clustering in urban plant communities than in arable communities. This result may also point to manmade disturbance working as a filter on plant communities, as many urban habitats experience even higher and more dynamic disturbance than agricultural habitats (Knapp *et al.*, 2012). In addition, the difference in change of NRI and NTI values between historical and contemporary relevés could be explained by the high increase in percentage of grassy species. If this happens, the long branches of the phylogenetic tree between monocotyledons and dicotyledons cause MPD values to increase disproportionally. In consequence, this would increase the NRI values.

Changes in traits

The environmental filters mentioned above not only diminished species richness and phylogenetic diversity but also influenced the diversity of plant functional traits in both arable and meadow communities. Some of the favoured traits in arable communities, such as seed longevity, short flowering period and annual lifecycle, can be directly linked with the high rate of disturbance in crop fields (Blaxter & Robertson, 1995; Diaz *et al.*, 1998; Thompson *et al.*, 1998; Robinson & Sutherland, 2002; Louault *et al.*, 2005). For instance, increases in disturbance frequency select for species and populations which either have already reproduced or which can re-establish from the seedbank (Zhang *et al.*, 1998). An annual lifecycle is mostly then an advantage if the disturbance is regular but of high impact, such as caused by tilling (Booth & Swanton, 2002). Additionally, we found an increase of grass species with increasing phylogenetic clustering. In the arable communities, this might be due to the filtering effect of broadleaf-selective herbicides. As they were designed to not affect cereals, grass weeds are not eliminated (Fryer & Chancellor, 1970; Wrucke & Arnold, 1985). In arable communities, we found changes not only of single functional traits but also of the composition of traits present in the local community. This is in line with other studies, which found changes in trait

composition due to intensification (José-Maria *et al.*, 2011) or different agricultural practices (Colbach *et al.*, 2014).

The percentage of grass species also increased with increasing phylogenetic clustering in meadow communities. This is possibly due to the influence of higher nutrient levels (Fig. 4), which allow for the growth of a denser canopy in which grasses have better competitive abilities (Ryser & Lambers, 1995). While the composition of traits changed for arable communities (see above), it stayed more or less constant in meadow communities. This is most likely caused by the fact that agricultural techniques did change less dramatically for meadows than for arable fields. Hence, weeds had a much higher level of filtering that influenced the selection of functional traits. Although todays' meadows are fertilized and harvested more frequently, the main filter – cutting vegetation - stayed the same (Dietl, 1995). However, this is only true for meadows that are not sown.

The loss of a large number of species and their associated traits could have large consequences on ecosystem services, such as shelter for beneficial organisms, nectar food resources for pollinating insects or protection from soil erosion (Swinton *et al.*, 2007; Isbell *et al.*, 2011). High phylogenetic and trait diversity as well as species richness help to maintain high resilience in ecosystems against changes in climate or (in this case) agricultural practice (Díaz *et al.*, 2007; Isaacs *et al.*, 2008). However, if diversity decreases, the ecosystem may become more unstable and could – at some point – no longer provide the expected services. As species losses were not compensated by neophytes, conservation measures need to be taken to ensure the functioning of agricultural ecosystems.

Conclusions

The species losses we found in Switzerland are similar to those reported for arable communities of Germany and Slovakia (Májeková *et al.*, 2010; Meyer *et al.*, 2013), suggesting that similar processes of environmental filtering are at work across Europe. This is probably also true for other countries

with intensive and highly mechanised agriculture as studies from Japan and the USA report similar results (Webster & Coble, 1997; Conn *et al.*, 2011; Yamada *et al.*, 2011). It is not clear what consequences the introduction of modern agricultural practices to developing countries will have. It is, however, likely that the worrying tendency of decreasing species and phylogenetic diversity spreads to these countries too. Therefore, Switzerland may exemplify what happens to agricultural plant diversity in countries with modern agriculture (although Swiss agriculture is more on the moderate side; eurostat, 2005; Herzog *et al.*, 2006) and what could happen all over the world. Our study clearly suggests that communities from which plant species are lost through environmental filtering, become more phylogenetic clustered (Kraft *et al.*, 2007). Additionally, if these environmental filters change over time, functional trait diversity and distribution will change as well.

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Biosketches

Nina A. Richner: is a PhD-student at Agroscope and the University of Zürich. She is interested in ecology and botany of agricultural ecosystems.

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Peter Linder researches the evolution and maintenance of plant biodiversity, with a special interest in the Cape and also African floras.

Author Contributions: H.P.L. and N.R. conceived the idea, N.R. collected and analysed the data and led the writing with contributions from all other authors

Tables

Table 1: Total number of families, genera and species in historical and contemporary Swiss meadows and arable fields.

		Number of		
		Families	**Genera**	**Species**
Meadows	**Historical**	56	247	566
	Contemporary	49	200	445
Arable fields	**Historical**	41	171	283
	Contemporary	35	139	212

Table 2: Percentage contribution to the total flora of the nine largest families in Swiss meadows and arable fields.

	Arable fields		**Meadows**	
	Historical	**Contemporary**	**Historical**	**Contemporary**
Asteraceae	13	13	13.5	12
Poaceae	11.5	16	10.5	11.5
Fabaceae	7.5	7.5	6	6
Brassicaceae	7.5	6	1.5	3
Caryophyllaceae	8	5	2.5	4
Lamiaceae	5.5	6	3	4
Polygonaceae	4	5	1.5	2
Scrophulariaceae	6.5	6	4.5	3.5
Rosaceae	2	3.5	4.5	6.5

Table 3: Mean (± standard error SE) net relatedness index (NRI) and nearest taxon index (NTI) of Swiss meadows and arable fields

	Habitat	**Mean NRI**	**SE**	**p**	**Mean NTI**	**SE**	**p**
All	Arable fields	0.88	0.05	<0.001	0.54	0.05	<0.001
	Meadows	-0.09	0.07		1.27	0.05	
Historical	Arable fields	0.91	0.06	<0.001	0.35	0.07	<0.001
	Meadows	-0.37	0.1		1.18	0.07	
Contemporary	Arable fields	0.85	0.08	<0.001	0.75	0.08	<0.001
	Meadows	0.19	0.09		1.36	0.08	

Table 4: Mean values (± standard error) of net relatedness index (NRI) and nearest taxon index (NTI) for pooled communities of Swiss arable fields and meadows

	Time	Mean	SE	p
Arable fields				
NRI	Historical	0.91	0.06	0.25
	Contemporary	0.85	0.08	
NTI	Historical	0.35	0.07	<0.01
	Contemporary	0.75	0.08	
Meadows				
NRI	Historical	-0.43	0.09	<0.001
	Contemporary	0.16	0.09	
NTI	Historical	1.06	0.07	<0.05
	Contemporary	1.29	0.07	

Table 5: Result of best GLM (delta AIC = 16.8) for the pooled net relatedness index (NRI) values using habitats (contemporary and historical arable fields and meadows) and functional traits (Indicator value for humidity and nutrients; Percentage per relevé of herbs: herbaceous plants without fabaceaea; fabaceaea; archaeophytes (introduced before AD 1500); competition or ruderal strategists (Grime, 1977); and plants flowering for one, three or four months) as explanatory variables. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

	Estimate	SD	
Intercept	-2.8478	0.646	***
Historical arable field	0.8393	0.1154	***
Contemporary meadow	-0.4109	0.1625	*
Historical meadow	-0.9288	0.1753	***
Indicator value humidity	1.3416	0.137	***
Percentage of annual plants	3.1658	0.7907	***
Indicator value nutrients	0.3156	0.1098	**
Percentage of herbs	-2.148	0.2328	***
Percentage of Fabaceae	-8.7467	0.6104	***
Percentage of archaeophytes	0.917	0.309	**
Percentage competition strategists	0.6401	0.4008	
Percentage ruderal strategists	-2.183	0.6584	***
Percentage flowering for one month	18.9541	4.1962	***
Percentage flowering for three months	0.741	0.2918	*
Percentage flowering for four months	-0.5947	0.383	

Table 6: Result of the best GLM (ΔAIC=14.7) for nearest taxon index (NTI) values using habitats (contemporary and historical arable fields and meadows) and functional traits (Indicator value for humidity and nutrients; Percentage per relevé of herbs: herbaceous plants without fabaceaea; fabaceaea; idiochrophytes (native or naturally immigrated species); archaeophytes (introduced before AD 1500); neophytes (neophyte: introduced after AD 1500); competition or stress strategists (Grime, 1977); plants with seeds with a longevity between 20 and 100years and plants flowering for three months) as explanatory variables. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

	Estimate	SD	
Intercept	1.002	0.9872	
Historical arable field	0.1114	0.1197	
Contemporary meadow	0.8408	0.1742	***
Historical meadow	0.9486	0.1916	***
Indicator value humidity	0.4784	0.1541	**
Indicator value nutrients	0.2494	0.1584	
Percentage of herbs	-1.5972	0.2631	***
Percentage of Fabaceae	-2.1884	0.6724	**
Percentage of idiochrophytes	-2.0499	0.8331	*
Percentage of neophytes	-1.6287	0.933	
Percentage of archaeophytes	-2.1058	0.8801	*
Percentage competition strategists	-0.5951	0.4192	
Percentage stress strategists	-2.1927	0.7855	**
Percentage seed longevity 20 to 100 years	0.4435	0.2947	
Percentage flowering for three months	1.0895	0.3113	***

Figures

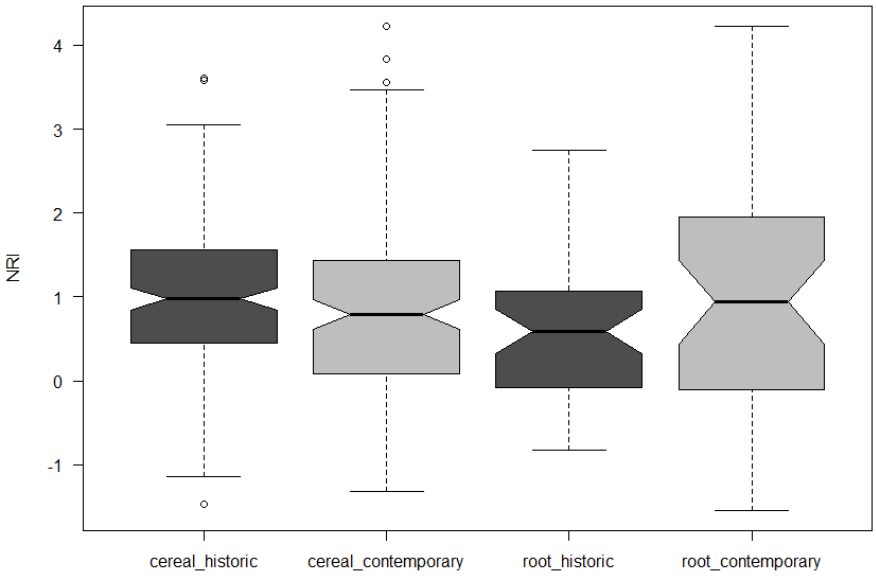


Fig. 1: Boxplot with notches showing the net relatedness index (NRI) values for Swiss plant communities in cereals and root crops in historical and contemporary arable fields

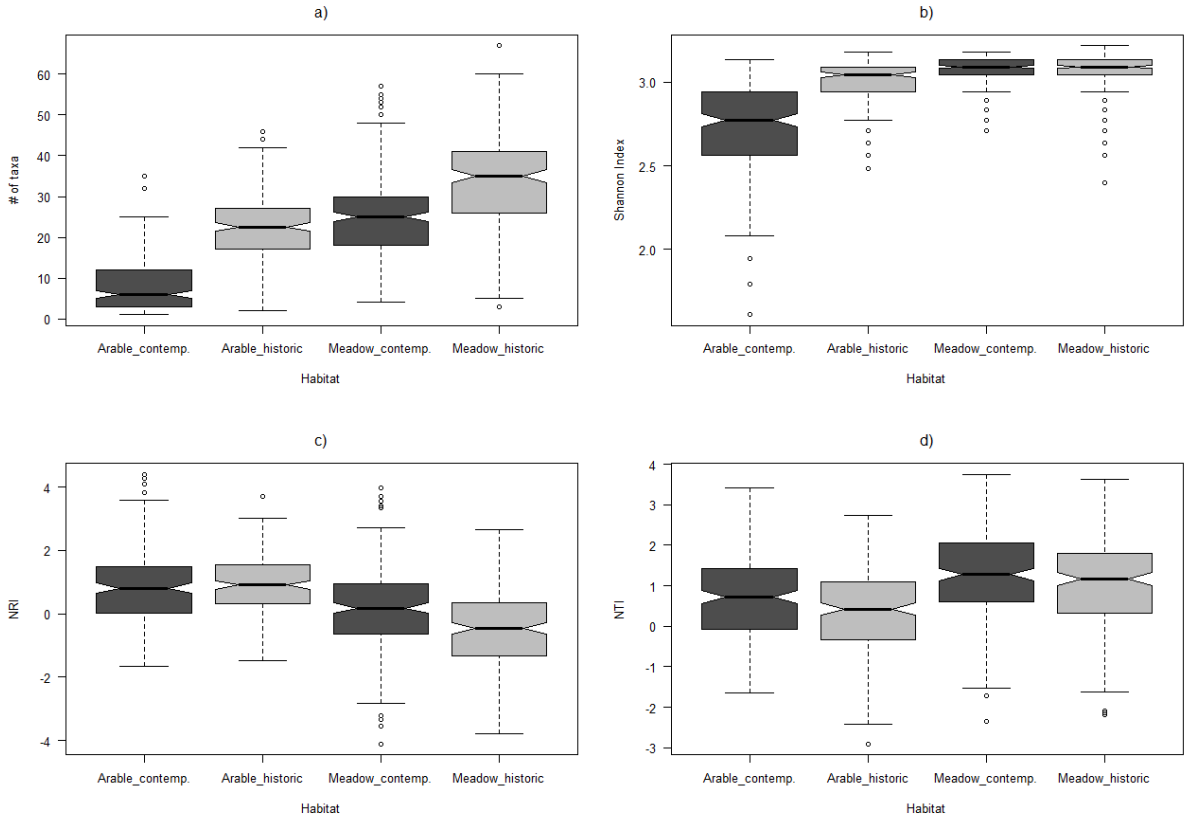


Fig. 9: Boxplots with notches for the four habitats (contemporary and historical arable fields and meadows) showing (a) mean number of taxa per relevé ($p < 0.001$), (b) average Shannon index of functional traits ($p < 0.001$), (c) average net relatedness index (NRI) values ($p < 0.001$) and (d) average nearest taxon index (NTI) values ($p < 0.001$).

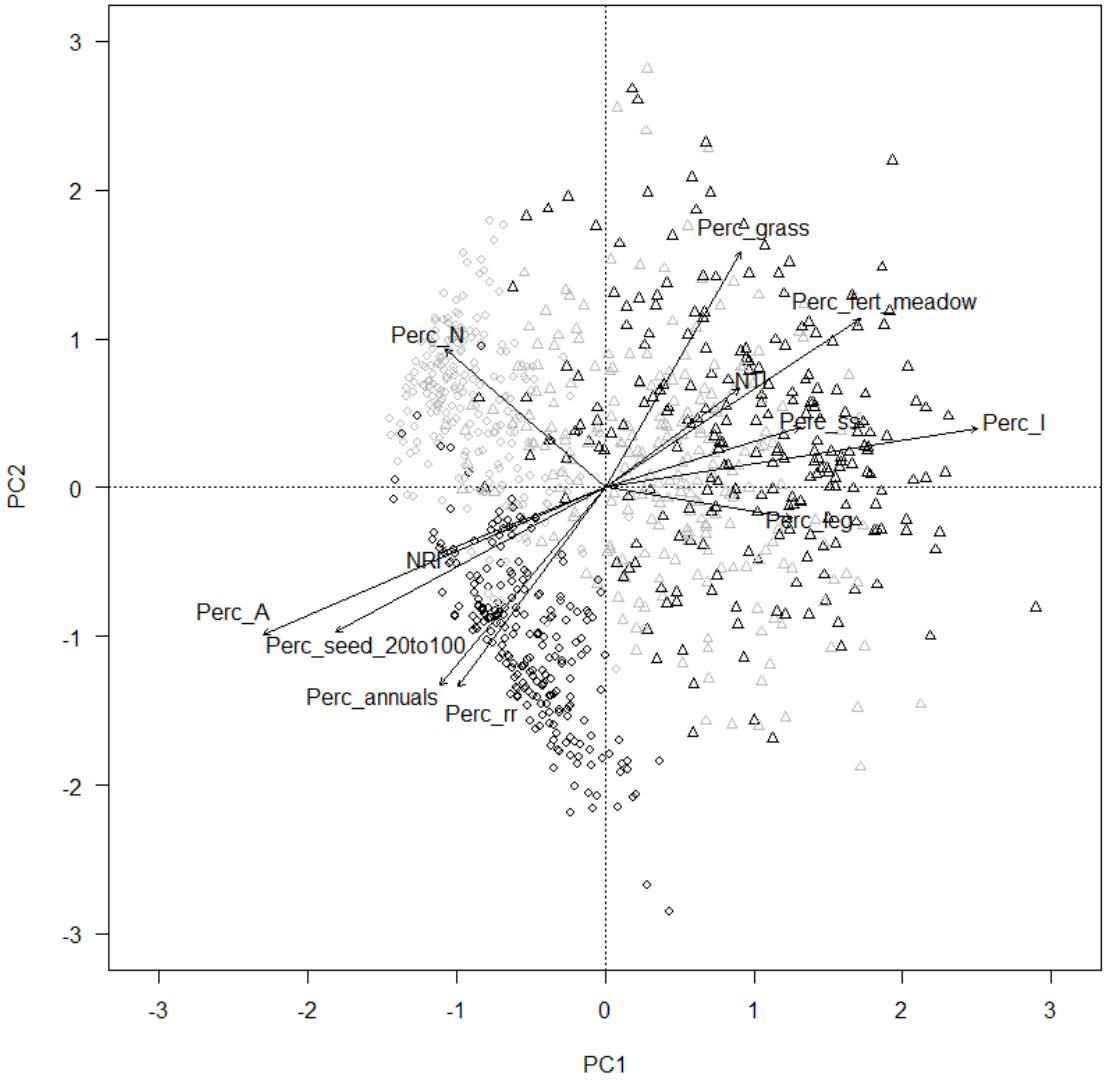


Fig. 3: PCA for functional traits of contemporary (grey) and historical (black) arable fields (circle) and meadow (triangle) communities. Arrows depicting the direction in which the value of trait increases: NRI: net relatedness index; NTI: nearest taxon index; Perc_: Percentage per relevé of: N: neophytes (neophyte: introduced after AD 1500); grass: monocotyledons; fert_meadow: plants characteristic for fertilized meadow communities; I: idiochrophytes (native or naturally immigrated species); leg: fabaceae; rr: ruderal strategists (Grime, 1977); annuals: plants with an annual life-cycle; seed_20to100: plants producing seeds with a longevity between 20 and 100 years; A: archaeophytes (introduced before AD 1500). Percentage of variation explained by PC1=55.9%; by PC2=24.5%.

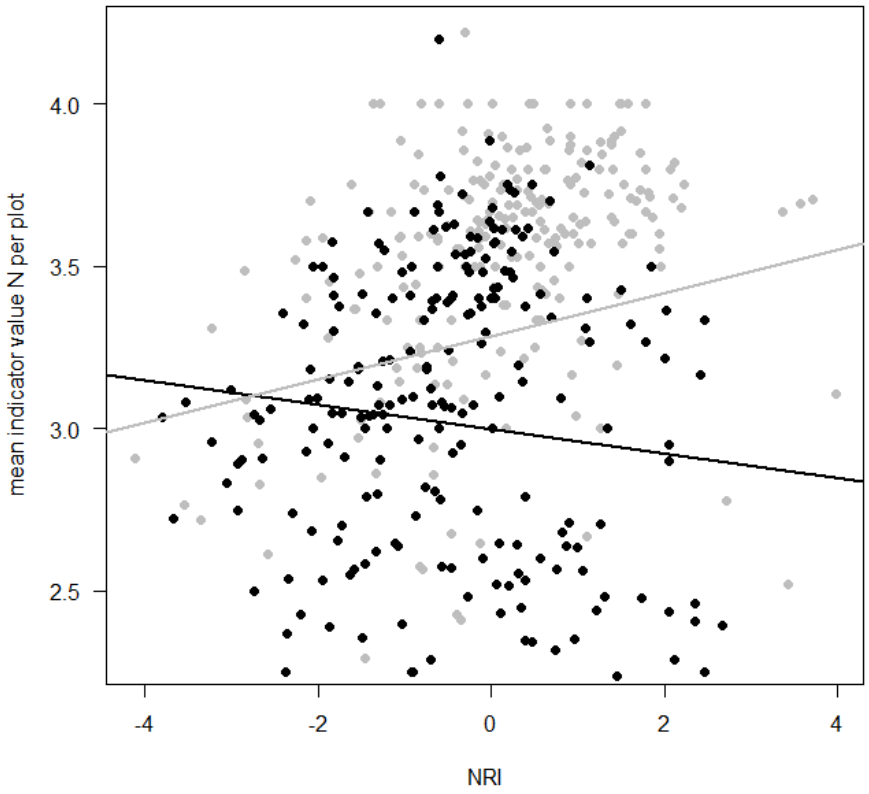
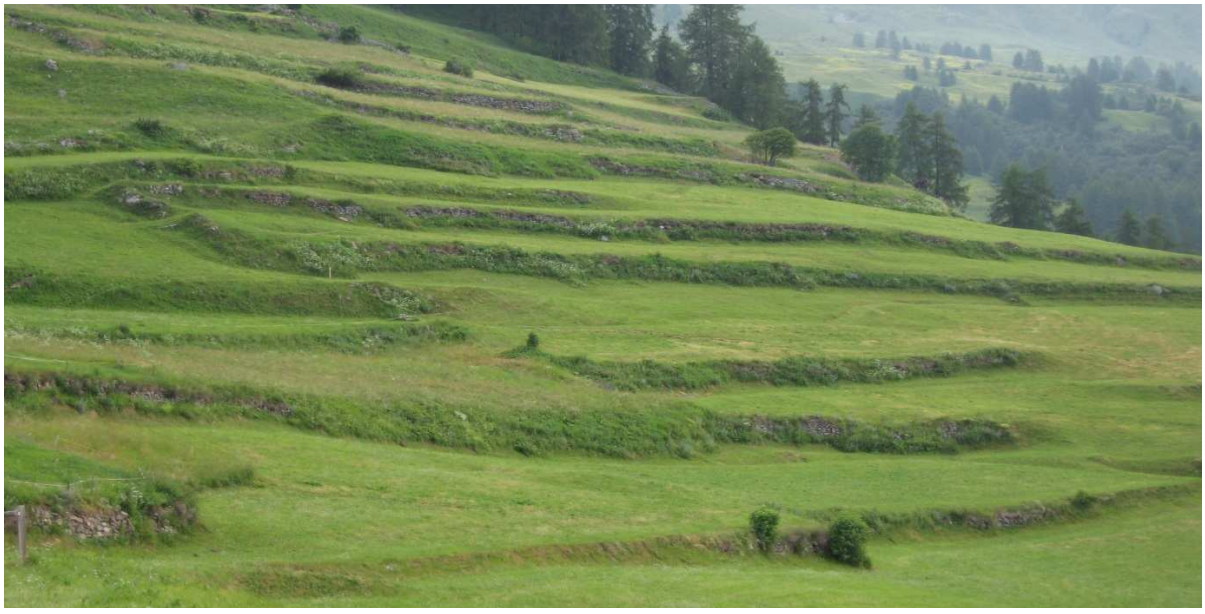


Fig. 4: Scatterplot of net relatedness index (NRI) values and the average indicator value for nutrients in meadows. grey: contemporary relevés (R2=0.13, p<0.001) ; black: historical relevés (R2=0.01, p=0.11)..

Chapter IV

Arable weed seed bank of grassland on former arable fields in mountain regions



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Manuscript

Abstract

The changes of agricultural practice during the last century resulted in high-input farming in lowlands and the abandonment of crop fields in marginally profitable mountain regions. In Switzerland, abandoned fields were converted into grassland, these fields had a rich historical flora and the few still existing fields there still belong to the most species rich. As many arable weeds produce long-living seeds abandoned fields nowadays converted to grassland should have a high potential to promote rare and threatened arable plants if tilled again. To test this hypothesis, 21 soil samples down to 20cm depth in each the centre and the border of 38 abandoned fields were taken respectively. The centre and border samples of each filed were each pooled and afterwards the present seeds washed out. These seeds were then sown in pots and germination monitored in a greenhouse during six months. Once a week, the seedlings were identified to species and removed. A total of 119 plant species were identified, 96 in the border and 89 species in the centre of former fields. Of these, 48 species were typical arable weeds. One was red listed in Switzerland. The total number of species as well as the number of arable weeds per former field was lower at higher its altitudes. Hence, the surveyed meadows have a small potential to promote threatened arable weeds if tilled again. Likely, the fields were not tilled for a too long time period and that therefore seeds were no longer viable. If conservation fields are established, the development of arable weeds has to be surveyed. If no threatened species grow spontaneously after a few years it should be considered to reintroduce the desired plants from nearby still existing species pools.

Keywords: conservation, restoration, segetal species, Swiss Alps

Introduction

The changes of agricultural practice during the last century resulted in high-input farming in lowlands and in the abandonment of fields in marginally profitable mountain regions (MacDonald et al., 2000). Abandoned fields were converted into grassland. In Switzerland, these fields had a rich flora on arable fields in historical times and the few still existing fields in these regions belong to the currently most species rich (Volkart, 1933, Richner et al., 2014). This is probably because many arable weeds need a low amount of nutrients and herbicides, which is still the case in these marginally profitable areas. Arable weeds adapted to low nutrient levels are often red-listed today (Moser et al., 2002). As it is not possible to achieve high yields from fields with low nutrient levels, they are at risk of being also converted to grassland which would eliminate the still existing arable weed flora. It is therefore important to promote arable farming (the production of cereal and root crops) in regions with low fertilizer input or low soil nutrient levels.

Arable fields are subject to frequent disturbance due to tillage and crop harvesting. The plants growing on these fields other than the crop itself are called arable weeds. Their lifecycle is adapted to disturbance. The seeds of arable weeds are buried when the field is tilled resulting in a different vertical distribution of seeds in the soil compared with undisturbed habitats (Bekker et al., 1998). Therefore some seeds in the seed bank do not germinate (Benech-Arnold et al., 2000, Baskin & Baskin, 2001). Hence, one survival strategy of arable weeds is to produce seeds with high longevity, being capable to germinate even after long time periods of burial (Schneider et al., 1994, Thompson et al., 1997, Thompson et al., 1998). Those buried seeds build the seed bank of which the weed flora is re-established every year. As weeds can have a high impact on crop yield, their seed bank is well studied (Brenchley & Warington, 1930, Roberts & Feast, 1973, Ball & Miller, 1989, Cavers & Benoit, 1989, Chauvel et al., 1989, Thompson et al., 1997). Most arable weeds produce seeds that are viable for about 20 to 100 years (Lewis, 1973, Barralis et al., 1988, Schneider et al., 1994, Thompson et al.,

1997). Up to 40% of weed species have seeds that can germinate after more than 50 years of dormancy (Wäldchen et al., 2005). This study was based on literature review and a field study that tilled fields that were lying fallow for 10, 15, 50 or 60 years. Still, there are big differences between species and depending on the method used to evaluate the longevity even within a species (Salzmann, 1939, Barralis et al., 1988, Wäldchen et al., 2005). Lutman (2002) estimated loss rates from seed banks between 20% and 40% per year with minimum and maximum rates of 9% and 60%. Values are usually higher in light soils than in heavy soils (Lutman et al., 2002). According to McCloskey et al. (1996), tilled fields have seed banks with a higher number of species and seeds with a longer lifespan than untilled fields. To break the dormancy of the seeds, environmental conditions must become favourable for germination. Such as more light, better aeration, alternated temperature or higher nutrient availability (Toole et al., 1956, Wesson & Wareing, 1969, Cavers & Benoit, 1989, Baskin & Baskin, 2001). These circumstances are met after tilling or other soil disturbances that bring buried seeds to the soil surface.

As many arable weeds produce long-living seeds, fields that were abandoned and converted to grassland should still have a high potential to promote rare and threatened arable weeds if they were tilled again. However, in arable land converted to grassland, seed density of weed species in the seed bank decreases by 40% in six years (Mrotzek & Schmidt, 1993, Albrecht, 2005, Albrecht & Auerswald, 2009). Hence, the further back the use of a particular field area as cropped land lies the more difficult the restoration of rare arable weeds becomes. Especially on nutrient rich soils, regeneration of weed species out of the seed bank is apparently hardly possible (Bischoff & Mahn, 2000, Kohler et al., 2011). Furthermore, only a small fraction of the seeds present in the seed bank can germinate after tillage as not all of them come to the surface. Thus, rare species might germinate in very low numbers (Traill et al., 2007, Flather et al., 2011). However, under low-nutrient conditions, the situation might be different. Recolonization by weeds on nutrient rich soils therefore usually

takes place out of relic occurrences in field margins or from neighbouring fields if available (Marshall & Moonen, 2002, Bischoff, 2005). When establishing conservation measures for arable weeds it is thus important to have suitable seed sources nearby.

In contrast to general studies on the behaviour of buried seeds, we found few published studies on the seed bank of abandoned cropped land (Dutoit et al., 2003, Wäldchen et al., 2005, Kohler et al., 2011). However, these studies lacked a reference to the original weed flora that grew before conversion to grassland. In this study, as we had access to 3'500 vegetation surveys conducted on arable fields from 1927 to 1985. By analysing the seed bank present at the same locations as historical surveys, we could directly compare the historical arable weed flora with its current occurrence in the seed bank. We tested the following hypotheses. (1) There are still arable weed species found in the soil of mountain grassland, that were once used as arable fields. (2) In the center of fields, less seeds of arable weed species persisted than in the border of former fields because field margins usually contain a larger and more species-rich arable flora (Marshall & Moonen, 2002). (3) Seed banks at locations with a historically high diversity of arable weeds still harbor more arable weed species than seed banks at locations with a formerly low-diversity weed flora. (4) As field under less profitable conditions such as steeper slopes and higher altitude were more often and earlier converted to grassland than fields under more profitable conditions (MacDonald et al., 2000) the number of arable weed species in the seed bank of former fields should also be influenced by slope and altitude, as a proxy to years since conversion to grassland.

Methods

Study area

The revisited former arable fields now turned to grassland were located in Switzerland between 300 and 1730 m above sea level in the cantons Ticino and Grisons (Fig. 1). The locations consisted of meadows from valley-bottom up to about mid-mountain slope. Meadows on slopes were mostly

located on old, traditional terraces. Soils were mostly shallow or intermediate in depth with a medium to high amount of stones (Swisstopo, 2014a). Mean annual temperature was between 3.5°C and 10°C (MeteoSchweiz, 2013). Annual precipitation amounted to 1000mm to 1700mm.

Selection of historical locations for seed bank samples

A large vegetation database exists at Agroscope INH. For a re-survey study (Richner, submitted), 700 locations where historical surveys or arable weeds in fields between 1927 and 1980 were selected by a stratified random sample from the whole dataset: the strata consisted of biogeographic region, historical author, Red List status and crop type. For identifying the location of historical surveys, we relied on the original historical references in combination with spatial analysis in ArcGIS (ESRI, 2009). In the cantons of Ticino and Grisons, we revisited 19 locations each where historical crop fields had been converted to grasslands.

Data collection

On the 38 plots chosen we measured seed-potential. Unfortunately, we had no information when fields were converted to permanent meadows. To have a rough estimate, we consulted historical aerial images available from 1956 onwards (Swisstopo, 2014b) and chose the year of the youngest picture showing no arable field at the location as the “first year” of conversion. As also aerial images were only available in black and white, the decision of whether there were still arable fields was often difficult. Therefore, the first picture where we were fairly sure that there were no fields no more was assigned youngest. The such estimated time since conversion was between 13 and 59 years.

Soils samples were taken at the end of September 2011 after the grass has been cut. Each site was divided in to field-centre and a field-border zone as field borders usually have a higher diversity of arable weeds (Fig. 2; Kleijn & Verbeek, 2000). Additionally, the seed bank of field borders could have been stocked by nearby ruderal habitats (Bischoff, 2005). The border zone consisted of the

outermost 3 m of the field was usually well defined by roads, hedges, ditches or walls. For each centre and border zone 21 soil cores of 2.5 cm diameter were taken to a depth of 20 cm (Dessaint et al., 1996, Smutný & Křen, 2003). The depth of 20cm was chosen, as the ploughing layer is usually that deep. The soil cores were evenly distributed on the zone area (Dessaint et al., 1991). We removed the turf from the soil samples- about 1.5 cm - as seed in this part would mostly be from the current vegetation. We pooled the soil cores of each zone for each field and stored them in a plastic bag in a cool box.

It was difficult to have the same area of the plots for all sampled fields. As we did not know how small the smallest field would be, we had to assume a "smallest" plot area in which the samples were afterwards distributed. The smallest sampled plot was about $8m^2$, meaning that the "centre" of this field was not existent according to our criteria of 3m border zone. Therefore, the border zone had to be chosen smaller as to generate a field centre we could then sample. The small sampled area might have positively influenced the precision of our sampling as we had a high number of soil cores on a small area (Wiles & Schweizer, 2002). However, the number of present arable weed species in bigger fields could have been underestimated as not the whole field was sampled.

We determined viable seeds in the soil cores by the seedling emergence method according to Ter Heerdt (Ter Heerdt et al., 1996). Per field zone 2 pots with a diameter of 13cm were used. The seeds and the soil left over after sieving were spread evenly in the pots in layers of about 7mm. No artificial germination stimuli like gibberelin were used. However, we introduced a cold temperature stratification to break dormancy. After 12 weeks in the greenhouse, the pots were placed in a dark room with a temperature of 5°C. Seedlings were identified according to Hanf (1999) and species determined, removed once a week. Plants that could not be identified were planted into separate pots and grown on until they could be identified. Grasses and sedges were distinguished to the family level. At the end of germination we estimated moss cover.

Statistical Analyses

All statistical analyses were done in R 3.1 using packages MASS and NLME (Venables & Ripley, 2002, Pinheiro et al., 2013; R Development Core Team, 2013). Taxa that could not be identified to species were only included in analyses of the total species number. Analyses were done once for all found species and once only for arable weed species. To test for differences in average species number between centre and border zones in fields pairwise, two-tailed t-tests were applied. We calculated generalised linear mixed models using species number or percentage of historically occurring species re-found in the seed bank per plot as response variable. Minimum time since the last cultivation of a location, zone in the field, slope, altitude and cover of moss was used as explanatory variables and field-ID as random effect. Slope and altitude were chosen as they also proxy for the time when a crop field was converted to grassland as fields at higher altitudes and slopes are less economic (Streifeneder, 2009). Cover of moss at the end of experiment was selected as extensive moss cover can hinder seeds to germinate (Jeschke & Kiehl, 2008). We selected the best model using the Akaike's Information (AIC) Criterion. Significance of generalised mixed models was assessed using likelihood-ratio tests.

Results

All species

In the historical surveys 141 species (69 typical arable weeds) were recorded with an average of 15.3 (±0.84) species per plot. Out of 3460 seedlings that germinated, a total of 119 plant species were identified, 96 in the border zones and 89 in the centre of former fields (Table 1). Per location, between 32 and 142 seeds germinated. In the Ticino, 101 species and in the Grisons 92 species were found. The interaction of slope and altitude had a negative influence on the total number of germinated species (Table 2). However, the number of species in the border zones not was not higher than that in field centres. The number of individual seedlings was positively correlated with

the total number of species in the sample while the interaction of slope and altitude had no influence (Table 3). From the border zone, the average number of individual seedlings was about seven higher than from samples in the field centre ($p<0.05$, $t = 1.745$). On average, we detected 12.1% (± 1.5% se) of the species of the historical surveys in the current seed bank, corresponding to none to five species per location. Of totally 49 re-found species 25 species were re-found on the same field (Appendix A). A list with all species re-found on the same field and their respective seed longevity can be found in Appendix B.

Typical arable weeds

Of all germinated species, 48 were typical arable weeds according to Landolt et al. (2010). One of these (*Gypsophila muralis* L.*)* was mentioned on the Red List of Switzerland (Moser et al., 2002). The three species most frequently re-found were *Chenopodium album L., Capsella bursa-pastoris (L.) Medik.* and *Viola arvensis Murray*. The single red listed species found, was not among the nine red listed species in the historical surveys. Of the 25 species re-found on the same field, 17 were arable weed species. The species number of arable weeds was lower the higher up in the mountains a field was located (Table 4). Also, the percentage of arable weeds of the total number of species per plot was negatively correlated with the altitude of a field was and by the number of species in the historical survey (Table 5). The correlation of altitude and number of arable weed species per sample is shown in Fig. 3. Altitude was positively correlated with the number of years since conversion to grassland ($R^2=0.07$, $p<0.05$). Whether the sample was taken in the border of fields or centres had no influence on the number of arable weed species germinated. Also the cover of moss and time since conversion to grassland had no influence on the number of arable weeds germinated . We found no effects of slope or altitude on the percentage of re-found species. However, the percentage of re-found species was higher the shorter the time period since the historical survey was (Table 6).

Discussion

Out of 119 plant species that were found in the seed bank of former arable fields conversed to grassland in this study, 48 species were typical arable weeds (Landolt et al., 2010) which supports our first hypothesis. Of these, one was mentioned on the Red List of threatened plant species of Switzerland (Moser et al., 2002). About 10% of all species as well as typical weeds recorded in historical surveys were present in the seed bank.

In line with our second hypothesis, the number of seedlings was higher in border zones than in centre zones of former fields. That it was as well positively correlated with the total number of species germinated is not surprising, as most if not all species were present in small seedling numbers: the higher the number of species was the higher was thus the number of seedlings. This could be explained by the usually high species numbers in the field border (Kleijn & Verbeek, 2000). In contrast, we showed that whether samples were taken in the border of former field or in field centres had no influence on the number of arable weed species that germinated. This result shows that, even if the field borders usually have a higher species diversity than field centres (Kleijn & Verbeek, 2000), this higher species diversity was not represented in the seed bank after some decades. This is likely because viable seeds get lost over the years (Lutman et al., 2002). The seed longevity of the arable weeds that germinated was mainly between 20 to 100 years (Landolt et al., 2010; Appendix A).

In accordance with the hypothesis three and four we found a correlation of altitude and the number of species in the historical surveys with the percentage of arable weed species in the seedbank. However, the direction of the correlation was opposite to the one we expected. This could be because higher altitudes that historically had higher species number were conversed to grassland longer ago. As seed density declines with increasing time since conversion, more seeds from the seed bank were lost (Thompson et al., 1998, Lutman et al., 2002, Wäldchen et al., 2005). The negative

correlation of altitude with the total number of arable weed species and the percentage of re-found species could base on weeds being generally adapted to warm climatic conditions (Holzner, 1984). Therefore, a decline of weed species in higher altitude is not surprising. Additionally, the conversion to grassland happened earlier the higher the altitude of a fields was. That slope did not correlate with the number or percentage of arable weed species in the seed bank could because most fields were situated on terraces. Therefore, the slope of the individual field had no influence on the point in time for conversion to grassland.

The correlation between percentage of arable weed species with the minimal elapsed time since conversion to meadow was not significant. Probably because the method used was too imprecise or because the conversion was so long ago (the youngest field about 30 years ago with one exception) that most arable seeds were anyway not viable anymore. Other studies done on former arable fields reported results from grassland that was converted between ten and 50 years ago. However, these studies made no comparison of germinated weeds and the original flora on these fields. The inaccuracy in this study was based on the long intervals between the dates of the aerial images and the difficulty to differentiate between grassland and arable land on the old aerial images. However, as the elapsed time between conversion to grassland and our study was fairly long, a small inaccuracy should not have an influence on the results. For further studies it would be advantageous if the exact year of conversion could be obtained from historical sources.

Can the seed bank of abandoned arable fields help to promote rare weeds?

With one exception (*Gypsophila muralis* L.), we did not find rare weed species in the seed bank. The method used is reputed to detect between 81% and 100% of the viable seeds present in soils (Ter Heerdt et al., 1996). It is therefore likely that we did miss no or only a very small number of rare species with viable seeds in our germination study. Most weed species have a patchy distribution within fields. However, because we sampled 21 evenly distributed soil cores per zone, the risk of

missing patchily distributed rare species should also be reduced in our study (Dessaint et al., 1991, Dessaint et al., 1996, Jones, 1998). Probably, the sample size of 19 fields per study region was too small to detect the seeds of threatened plants. However, even for germinated species the risk to not detect them, even if they are present is about 11% (Kéry et al., 2006). The three species that germinated with a seed longevity of less than five years were typical plants of meadows namely *Bellis perennis* L., *Dactylis glomerata* L. and *Taraxacum officinale* aggr. (Landolt et al., 2010); their seed bank was thus regularly re-stocked regularly with new seeds since the conversion of arable fields to grassland.

Based on the historical surveys, nine rare weed species could principally have been re-found However, only six of them had a seed longevity of 20 to 100 years (Landolt et al., 2010). It is therefore likely that the fields were not tilled for a too long time period and that therefore the viable seed bank was depleted. The seed longevity of the arable weeds that germinated was mostly between 20 to 100 years, but also included four species with seed longevity of over 100 years. We found no arable weeds among the seedlings with seed longevity shorter than 20 years. On average 9.4 % (± 1.4%) of the species in the historical survey were re-found as viable seeds in the seed bank. However, also species that were not re-found have a high seed longevity and could, even if they were not detected in the present study, germinate if the field would be tilled again. A seed bank analysis on former arable land that was turned to meadows in the Alpine Lower Engadin came to the same conclusion (Battaglia & Hodler, 2008). In soil samples of twelve meadows, they found 18 typical arable weed species of which one (*Silene noctiflora* L.) was red listed. It seems therefore that while common species can be restored without many difficulties from the seedbank the reestablishment of rare and threatened arable weed species is a much greater challenge. This conclusion is in line with a study in France (Dutoit et al., 2003), stating it would be difficult to restore rare arable weeds by re-cultivating meadows after just ten years since conversion to grasslands.

In contrast to our study, the Alpine fields in Valais that have been taken into crop-rotation again, showed a relatively high amount of germination of rare arable weeds (Kohler et al., 2011). Likely the soil-conditions had been better in the Valais, because they were extensively managed grasslands since crop production stopped (Kohler et al., 2011). Therefore, soils contained a lower amount of nutrients thus increasing longevity of seeds (Bischoff & Mahn, 2000). In our cope, most meadows sampled were fairly intensively managed with potentially higher nutrient input. Additionally, soils in Valais are dryer, which also increases seed longevity (Thompson et al., 1998).

Despite restoration of the arable weed flora from soil seed bank seems hardly possible, some successful projects relying on different approaches for the conservation of arable weeds have been implemented in Switzerland and elsewhere. For instance, if there are suitable source populations nearby (Bischoff & Mahn, 2000, Bischoff, 2005), restoration through re-ploughing is feasible (e.g. Jeizinen VS; Kohler et al., 2011). In contrast, most of the grasslands surveyed in this study had a small potential for re-immigration of typical and rare arable weeds, because local species pools were no longer available. If these grasslands would be ploughed again, desired weed species would have to be introduced again using an appropriate seed-mixture. This approach is successfully used in Germany in the project “100 fields for diversity” (Meyer et al., 2008). Nevertheless, one has to account for the fact that seed-mixtures of arable weeds may contain non-adapted, non-regional genotypes (Vander Mijnsbrugge et al., 2010). Their sowing would also decrease the original genetic diversity if regional genotypes still exist. It would therefore be advantageous to perform a seed bank analyses of meadows that are intended to be tilled again to see if the conversion would be successful. From the seed bank analyses it would then be possible to make a model to predict the emerging flora (Zhang et al., 1998, Otto et al., 2007).

Conclusion

Due to the high seed longevity or arable weeds, the arable flora should among the easiest communities to re-establish. Even if we found only one threatened species in the soil samples, the possibility that rare species were underrepresented in the sample exists (Dessaint et al., 1996, Jones, 1998). As a study from the Valais shows, a highly diverse arable flora with threatened species can evolve if grassland on former arable land is tilled again. In further studies, former fields in other parts of the Alps, preferably on calcareous, dry soils (Bischoff & Mahn, 2000, Kohler et al., 2011), should be taken into cultivation again to get a more general picture.

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Figures

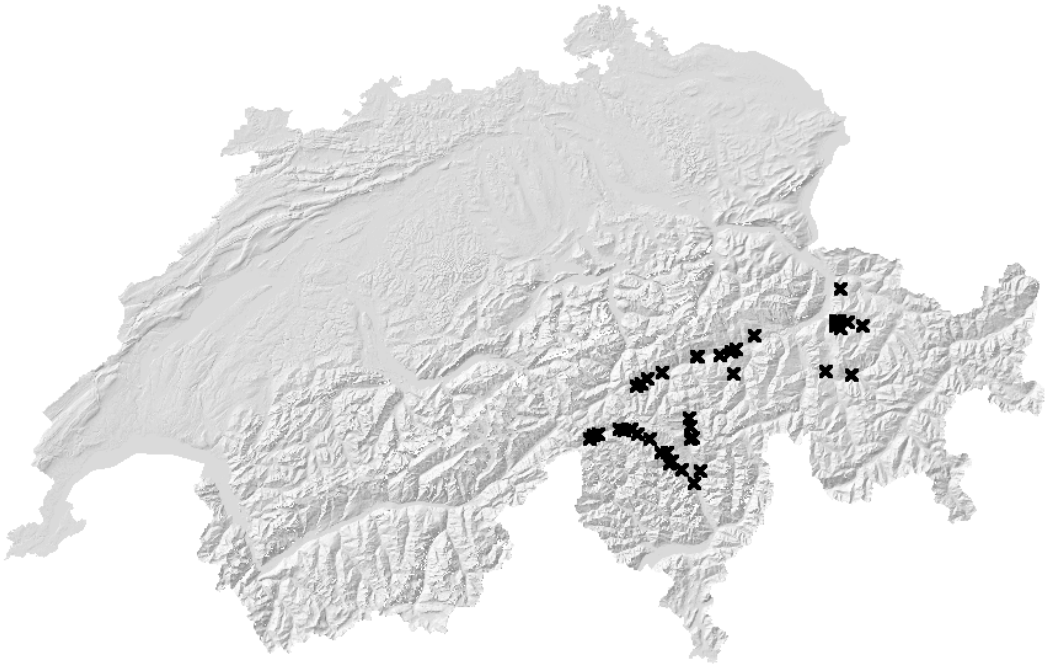

Fig. 1: Locations of the sampled locations in the cantons Grisons and Ticino (geodata © swisstopo).

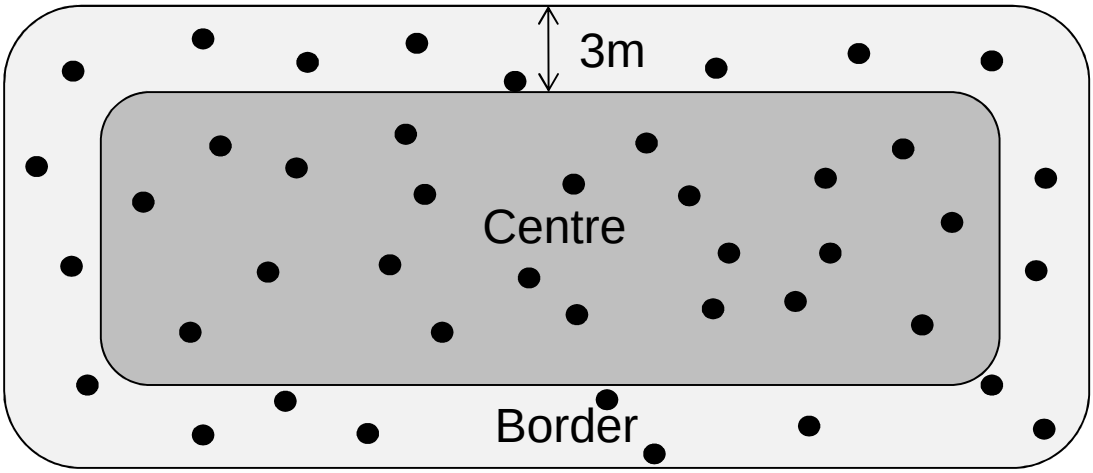

Fig. 2: Schematic representation of the sampling of the soil-cores in the centre and border zones of former fields.

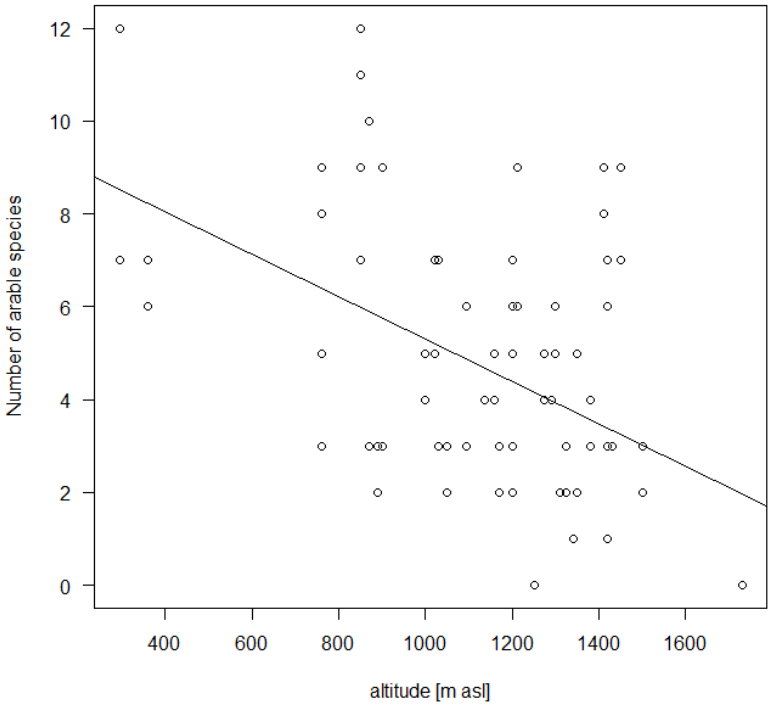

Fig. 3: Correlation of altitude and the number of arable species that germinated from the soil samples (p_{GLMM}<0.001).

Tables

Table 1: Number of total germinated species and germinated arable weed species in field centres, field borders and in total

	Total number of species	Number of arable weed species
Centre	89	35
Border	96	42
Total	119	48

Table 2: Results from the best generalized linear mixed model (ΔAIC 34) of zone in the field and the interaction of slope and altitude on the number of species. Random effect: location of the plot (SD intercept 3.07, SD residual 2.72); Two groups, 76 observations; Significance p< 0.05 *, <0.001 ***

	Value	SE	DF	
Intercept	15.68	1.09	37	***
Field centre	-0.34	0.45	37	
Altitude: Slope	-0.0001	0.00005	36	*

Table 3: Results from the best generalized linear mixed model (ΔAIC 37) of zone in the field, number of germinated species and years since conversion to grassland on the number of individual seedlings; (SD intercept 5.74, SD residual 17.21); Two groups, 76 observations; Significance p< 0.01 **, <0.001 ***

	Value	SE	DF	
Intercept	29.69	9.69	36	**
Field centre	-6.90	3.95	36	.
Number of germinated species	2.14	0.51	36	***
Altitude: Slope	-0.24	0.18	36	

Table 4: Results from the best generalized linear mixed model (ΔAIC 38) of altitude on the number on emerged arable weed species. (SD intercept 1.92, SD residual 1.69); Two groups, 76 observations; Significance p<0.001 ***

	Value	SE	DF	
Intercept	9.86	1.48	38	***
Altitude	-0.01	0.001	36	***

Table 5: Results from the best generalized linear mixed model (ΔAIC 26) of field centre or border and altitude on the percentage of arable weed species. (SD intercept 11.5, SD residual 7.76); Two groups, 76 observations; Significance p< 0.05 *, p< 0.01 **,p <0.001 ***

	Value	SE	DF	
Intercept	78.25	10.75	37	***
Field centre	-2.98	1.78	37	
Altitude	-0.03	0.01	35	**
Number of species in historical survey	-0.93	0.4	35	*

Table 66: Results from the best general linear model (ΔAIC 6) on the percentage of re-found species of the historical survey with the year of the historical survey; Significance p< 0.05 *

	Estimate	SE	
Intercept	-1104.66	435.92	*
Year of historical survey	0.58	0.23	*

Appendix

Appendix A: Frequency of species recorded in the historical surveys and germinated from the soil seed bank in 2011.

Species name	Frequency in historical surveys	Frequency of seeds in the soil samples
Ajuga reptans L.	0	2
Allium carinatum L. subsp. *carinatum*	0	1
Arabis ciliata Clairv. /cf.	0	2
Arabis hirsuta (L.) Scop.	0	3
Arrhenatherum elatius (L.) J. & C. Presl	0	1
Athyrium filix-femina (L.) Roth	0	2
Atropa bella-donna L.	0	1
Betula spec.	0	5
Brachypodium spec. /cf.	0	1
Bromus hordeaceus L.	0	1
Buddleja davidii Franch.	0	2
Campanula rhomboidalis L.	0	8
Campanula spec.	0	2
Cardamine hirsuta L.	0	5
Carex spec.	0	6
Cerastium glomeratum Thuill.	0	3
Chenopodium bonus-henricus L.	0	3
Chenopodium polyspermum L.	0	3
Chrysanthemum leucanthemum L.	0	4
Cyclamen purpurascens Mill.	0	14
Daucus carota L.	0	2
Epilobium fleischeri Hochst.	0	1
Epilobium montanum L. /cf.	0	1
Erigeron annuus (L.) Pers.	0	3
Erophila obconica de Bary /cf.	0	2
Euphrasia spec.	0	1
Galinsoga ciliata (Raf.) S. F. Blake	0	1
Galium album Mill.	0	4
Geranium molle L.	0	2
Geranium pyrenaicum Burm. f.	0	2
Geranium robertianum L.	0	1
Gypsophila muralis L.	0	1
Hypericum perforatum L.	0	2
Juncus articulatus L.	0	2
Juncus spec.	0	14
Knautia spec.	0	18
Leontodon helveticus Mérat	0	1
Leontodon spec. /hisp	0	2
Leucanthemum vulgare aggr.	0	11
Lolium perenne L.	0	10
Luzula spec.	0	1
Lysimachia nummularia L.	0	25
Matricaria recutita L.	0	1

Species name	Frequency in historical surveys	Frequency of seeds in the soil samples
***Medicago sativa* L.**	0	3
***Oxalis fontana* Bunge**	0	20
***Plantago major* L.**	0	15
***Poaceae* spec.**	0	36
***Portulaca oleracea* L.**	0	2
***Potentilla neumanniana* Rchb. /cf.**	0	1
***Potentilla reptans* L.**	0	8
***Ranunculus acris* L. subsp*. friesianus* (Jord.) Syme**	0	18
***Rubus* spec.**	0	4
***Sagina procumbens* L.**	0	6
***Selaginella helvetica* (L.) Link**	0	1
***Silene flos-cuculi* (L.) Clairv.**	0	1
***Solanum nigrum* L.**	0	1
***Spergularia rubra* (L.) J. & C. Presl**	0	4
***Tanacetum vulgare* L.**	0	1
undistinguishable	0	14
***Verbascum thapsus* L.**	0	1
***Verbena officinalis* L.**	0	1
***Veronica beccabunga* L.**	0	4
***Veronica officinalis* L.**	0	1
***Viola reichenbachiana* Boreau**	0	1
***Rumex obtusifolius* L.**	1	12
***Urtica dioica* L.**	1	12
***Veronica persica* Poir.**	3	32
***Alchemilla vulgaris* aggr.**	2	18
***Bellis perennis* L.**	2	17
***Cerastium fontanum* Baumg. *subsp. vulgare* (Hartm.) Greuter & Burdet**	3	25
***Anthoxanthum odoratum* L.**	1	8
***Dactylis glomerata* L.**	3	17
***Epilobium collinum* C. C. Gmel.**	1	5
***Silene vulgaris* (Moench) Garcke**	5	22
***Rumex alpestris* Jacq.**	3	13
***Holcus lanatus* L.**	1	4
***Rumex acetosella* L.**	2	8
***Plantago lanceolata* L.**	5	17
***Clinopodium vulgare* L.**	1	3
***Rumex acetosa* L.**	1	3
***Taraxacum officinale* aggr.**	8	24
***Trifolium repens* L.**	13	36
***Trifolium pratense* L.**	8	19
***Arenaria serpyllifolia* L.**	8	18
***Capsella bursa-pastoris* (L.) Medik.**	12	24
***Chaenorrhinum minus* (L.) Lange**	1	2
***Leontodon autumnalis* L.**	1	2
***Lamium purpureum* L.**	2	3
***Sonchus oleraceus* L.**	3	4
***Amaranthus retroflexus* L.**	1	1

Species name	Frequency in historical surveys	Frequency of seeds in the soil samples
***Carum carvi* L.**	1	1
***Conyza canadensis* (L.) Cronquist**	3	3
***Geranium pusillum* L.**	1	1
***Glechoma hederacea* L.**	1	1
***Myosotis arvensis* Hill**	10	10
***Plantago media* L.**	1	1
***Polygonum lapathifolium* L.**	1	1
***Stellaria media* (L.) Vill.**	9	9
***Viola arvensis* Murray**	20	16
***Chenopodium album* L.**	24	17
***Rumex alpinus* L.**	3	2
***Achillea millefolium* aggr.**	16	8
***Anagallis arvensis* L.**	2	1
***Festuca rubra* L.**	2	1
***Polygonum aviculare* L.**	10	5
***Holcus mollis* L.**	3	1
***Sonchus asper* Hill**	3	1
***Heracleum sphondylium* L.**	7	2
***Sinapis arvensis* L.**	4	1
***Vicia hirsuta* (L.) Gray**	5	1
***Euphorbia helioscopia* L.**	13	1
***Fallopia convolvulus* (L.) Á. Löve**	28	2
***Galeopsis tetrahit* L.**	33	1
***Aegopodium podagraria* L.**	8	0
***Aethusa cynapium* L.**	2	0
***Agropyron repens* (L.) P. Beauv.**	7	0
***Agrostemma githago* L.**	9	0
***Agrostis capillaris* L.**	4	0
***Agrostis stolonifera* aggr.**	1	0
***Anchusa arvensis* (L.) M. Bieb.**	1	0
***Anthemis arvensis* L.**	2	0
***Anthyllis vulneraria* L.**	1	0
***Apera spica-venti* (L.) P. Beauv.**	4	0
***Artemisia vulgaris* L.**	1	0
***Atriplex patula* L.**	1	0
***Avena fatua* L.**	1	0
***Avena strigosa* Schreb.**	1	0
***Brassica rapa* L. *subsp. campestris* (L.) A. R. Clapham**	4	0
***Bromus arvensis* L.**	1	0
***Buglossoides arvensis* (L.) I. M. Johnst.**	1	0
Campanula patula* L. *subsp. patula	1	0
***Campanula rapunculoides* L.**	8	0
***Centaurea scabiosa* L.**	2	0
***Chaerophyllum aureum* L.**	1	0
***Cirsium arvense* (L.) Scop.**	4	0
***Convolvulus arvensis* L.**	18	0
***Crepis capillaris* Wallr.**	3	0
***Cynosurus echinatus* L.**	1	0

Species name	Frequency in historical surveys	Frequency of seeds in the soil samples
Echinochloa crus-galli **(L.) P. Beauv.**	1	0
Echium vulgare **L.**	1	0
Equisetum arvense **L.**	16	0
Euphorbia peplus **L.**	1	0
Euphrasia rostkoviana **Hayne subsp.** ***montana*** **(Jord.) Wettst.**	1	0
Fagopyrum tataricum **(L.) Gaertn.**	3	0
Festuca arundinacea **Schreb.**	1	0
Fragaria vesca **L.**	2	0
Fumaria officinalis **L.**	2	0
Galinsoga parviflora **Cav.**	1	0
Galium aparine **L.**	13	0
Galium spurium **L.**	7	0
Galium vailantii **DC.**	2	0
Geranium sylvaticum **L.**	2	0
Hieracium lactucella **Wallr.**	1	0
Hypericum maculatum **Crantz**	3	0
Knautia arvensis **(L.) Coult.**	3	0
Knautia dipsacifolia **Kreutzer**	2	0
Lamium album **L.**	1	0
Lamium amplexicaule **L.**	1	0
Lapsana communis **L.** ***subsp. communis***	5	0
Lathyrus pratensis **L.**	1	0
Leontodon hispidus **L.**	2	0
Lolium multiflorum **Lam.**	1	0
Lotus corniculatus **L.**	3	0
Medicago lupulina **L.**	6	0
Mentha arvensis **L.**	10	0
Myosotis ramosissima **Rochel**	3	0
Odontites vernus **(Bellardi) Dumort.** ***subsp. serotinus*** **Corb.**	3	0
Papaver rhoeas **L.**	1	0
Pastinaca sativa **L.**	1	0
Phyteuma ovatum **Honck.**	1	0
Pisum sativum **L.** ***subsp. arvense*** **(L.) Asch. & Graebn.**	3	0
Poa annua **L.**	1	0
Poa pratensis **L.**	3	0
Poa trivialis L.	5	0
Polygonum bistorta L.	2	0
Polygonum mite Schrank	2	0
Polygonum persicaria **L.**	11	0
Ranunculus acris **L.** ***subsp. acris***	3	0
Ranunculus repens **L.**	4	0
Raphanus raphanistrum **L.**	8	0
Rhinanthus alectorolophus **(Scop.) Pollich**	1	0
Scleranthus annuus **L.**	2	0
Sedum annuum **L.**	1	0
Sedum sexangulare **L.**	1	0
Setaria pumila **(Poir.) Roem. & Schult.**	1	0
Setaria viridis **(L.) P. Beauv.**	4	0

Species name	Frequency in historical surveys	Frequency of seeds in the soil samples
***Sherardia arvensis* L.**	4	0
***Silene dioica* (L.) Clairv.**	3	0
Silene nutans* L. *subsp. nutans	1	0
***Silene pratensis* (Rafn) Godr.**	2	0
***Solanum tuberosum* L.**	1	0
***Sonchus arvensis* L.**	3	0
***Spergula arvensis* L.**	4	0
***Stachys palustris* L.**	3	0
***Stellaria graminea* L.**	1	0
***Thlaspi arvense* L.**	1	0
***Trifolium campestre* Schreb.**	1	0
***Trisetum flavescens* (L.) P. Beauv.**	1	0
***Tussilago farfara* L.**	1	0
***Veronica agrestis* L.**	5	0
***Veronica arvensis* L.**	4	0
***Veronica chamaedrys* L.**	2	0
***Vicia cracca* L.**	25	0
***Vicia sativa* L.**	3	0
***Vicia sepium* L.**	1	0

Appendix B: Frequency and seed longevity according to Landolt et al. (2010) of species re-found at the same location in historical surveys and contemporary soil seed banks.

Species name	Frequency [n=38]	Seed longevity
***Anagallis arvensis* L.**	2	>100 years
***Arenaria serpyllifolia* aggr.**	4	20 to 100 years
***Bellis perennis* L.**	3	1 to 5 years
***Capsella bursa-pastoris* (L.) Medik.**	9	20 to 100 years
***Cerastium fontanum* Baumg.**	3	>100 years
***Chenopodium album* L.**	13	>100 years
***Conyza canadensis (*L.) Cronquist**	3	5 to 20 years
***Dactylis glomerata* L.**	2	1 to 5 years
***Euphorbia helioscopia* L.**	2	20 to 100 years
***Fallopia convolvulus* (L.) Á. Löve**	2	20 to 100 years
***Galeopsis tetrahit* L.**	2	20 to 100 years
***Holcus lanatus* L.**	2	20 to 100 years
***Lamium purpureum* L.**	2	>100 years
***Myosotis arvensis* Hill**	5	20 to 100 years
***Plantago lanceolata* L.**	4	5 to 20 years
***Rumex acetosella* L.**	2	20 to 100 years
***Rumex alpestris* Jacq.**	2	20 to 100 years
***Sinapis arvensis* L.**	2	20 to 100 years
***Stellaria media* (L.) Vill.**	3	20 to 100 years
***Taraxacum officinale* aggr.**	3	1 to 5 years
***Trifolium pratense* L.**	6	20 to 100 years
***Urtica dioeca* L.**	2	20 to 100 years
***Veronica persica* Poir.**	3	20 to 100 years
***Vicia hirsuta* (L.) Gray**	2	20 to 100 years
***Viola arvensis* Murray**	8	20 to 100 years

Conclusions

I found a decline of 65% in average species number per plot on Swiss arable fields in the last 90 years. Across Europe, the average number of arable species per plot declined by about 20% during the last 75 years. Potentially, this is due to various causes such as higher fertilizer and herbicide input or generally more intensive farming systems (Stoate et al., 2001). Not only did species number decrease, also the number of plant families decreased and plant communities in agricultural habitats are more phylogenetically clustered today than in the past. Additionally, the composition of plant functional traits changed. This study also shows that the influence of functional traits of the plant species on losses and gains in the species pool of arable plants still rests to be determined. Without such information on functional traits, it is very difficult to definitively disentangle the processes behind species decline, although such knowledge is essential in order to preserve biodiversity on arable land. A first clue on this aspect is given by the change in trait composition due to the filtering effect of the changing agricultural practice.

Species losses in arable weed communities happened in Switzerland as well as across Europe. From other countries with modern agricultural practices, like Japan and the USA, similar results are reported (Webster & Coble, 1997, Conn et al., 2011, Yamada et al., 2011). This suggests that similar processes of environmental filtering are at work across the industrialised countries. If developing countries adopt these modern farming systems the arable weed communities in these countries will probably decrease in species and phylogenetic diversity as well. In European countries, increases in average species number per plot since 1980s suggest, that measures taken to conserve biodiversity in agricultural landscapes might have a positive influence on the richness of arable plant species. Assuming this, it is important, that those agri-environmental schemes are adopted alongside with the modern agricultural practices.

Arable weeds are an important ecological good (Gerowitt et al., 2003). A high diversity of plants in arable habitats is therefore of great importance for the stability and functioning of the agricultural ecosystem and the services coming thereof (Isaacs et al., 2008, Isbell et al., 2011, Storkey et al., 2013). Agricultural land covers about 40% of the land area in Europe (Georgieva & Martins, 2012) and is thus one of the biggest biomes in Europe. Due to its importance, the stability of this ecosystem is of particular importance. This stability is not only threatened by the loss of weed species characteristic to traditional farming practices but also by the increase of newly introduced species. However, these introductions could also pose new chances for production and nature conservation. Invasive species could cause a loss of yield but could also constitute new food resources for beneficial organisms. As arable fields are a highly and regularly disturbed habitat, changes in floristic composition of weeds happen fast. Therefore, trends can – if monitored - be detected rapidly and actions against potential threats can be taken quickly.

The dramatic decline in number and frequency of arable weed species found in this study indicates that more focussed conservation measures are necessary to ensure the survival of rare and threatened weed species. As agri-environmental measures help to promote the plant species richness in agricultural habitats (Kleijn et al., 2006, Marshall et al., 2006), this is a valuable approach for conservation. However, the amount of biodiversity promotion areas in arable fields in Switzerland amounts to only 2% of all registered biodiversity promotion areas, which is only 0.6% of the total acreage of arable fields in Switzerland (BLW, 2013). Therefore, it is important to increase the extent of arable biodiversity promotion areas. Additionally, other measures for the protection of arable weeds must be taken (Rey Benayas & Bullock, 2012). Due to their adaptation to crops and farming practices arable weeds need very specific concepts for promotion; and so classical nature protection areas might not be effective. These concepts could consist of new categories of landscape or farm types, which in the future could be supported with specific contributions by the Swiss agricultural

policy or which could be used for a consumers label. Measures to promote rare arable weeds should not only take place in high-diversity regions. Firstly, specific measures in high-diversity regions have already been implemented (e.g. Staatsrat des Kantons Wallis, 1999, Agrofutura, 2012). Secondly, it is important, that regions with a historically rich arable flora which is nowadays depauperate find attention. In these regions rare weeds may probably still be re-established from the seedbank. Therefore, more general measures like are needed as well. Still, even if those measures are taken, it is difficult to spontaneously restore rare species in an intensively-used agricultural landscape. Mainly because regional species pools are depauperate due to the long continuity of high input of herbicides and mineral fertilizers. Hence, it might be a possibility is to install more, larger and wider unsprayed field borders to enhance the chance that rare species can germinate from the seedbank. Another possibility would be to use seed mixtures for establishing a diverse arable flora in a region. However, seed-mixtures of arable weeds sown in ecological compensation areas may contain non-adapted non-regional genotypes (Vander Mijnsbrugge et al., 2010). This would weaken the regional gene pool if the respective species is still present locally. Another problem are the less favourable arable weeds. Herbicide resistant species, for example, could grow in high densities and might therefore reduce yields. To ensure production, potentially harmful weeds for Switzerland such as *Apera spica-venti* P. B.*, Elymus repens* Gould*, Alopecurus myosuroides* Houds.*, Galium aparine* L. or *Cirsium arvense* Scop. should be monitored on conservation fields.

To have a proper overview on the Swiss arable flora it is necessary to sample fields of all important crop types in Switzerland. ,Studies need to be done for example in oilseed-rape, corn and vegetables, to see if rare species do also occur there. Up to now those crops have rarely been surveyed for weed diversity. Additionally, newer studies of vineyards are needed. This overview on modern arable weed communities could give a valuable base to monitor the introduction of new species.

The species and phylogenetic diversity of arable flora of Switzerland and Europe are threatened. As arable weeds play an important role in the agricultural ecosystem. Their conservation and promotion is essential. Hence, measures must be taken that aim at those targets without threatening the food production.

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Summary

Chapter 1

During the last decades, agricultural practices have changed dramatically. Today, the fields are managed mechanically, and industrial fertilizer and herbicides are applied. This intensification has on one hand increased yields but on the other hand plants and animals living in the agricultural landscape were repressed or got extinct. Therefore, the introduction of agri-environmental schemes (wildflower strips, set-asides) was decided in Europe during the 1980s. These schemes were intended to promote the natural communities of arable fields. To show the changes in the arable flora in a bigger context, a meta-analysis was conducted for data across Europe. A meta-analysis compares the outcome of all traceable studies that were conducted on a specific topic. Hence, a reliable conclusion about the underlying effect can be drawn. Therefore, internet databases were searched for studies that were carried out on arable fields in Europe comparing historic and contemporary vegetation surveys. A total of 32 studies corresponded with the criteria, yielding 53 datasets. The studies compared vegetation surveys from 1939 to 2007. Averaged over these datasets the species number per plot of arable plants declined by about 20%. However, twelve of these datasets showed an increase in average species number per plot. All studies that started after 1980 showed an increasing average species number. Plant species preferring nutrient rich sites, neophytes, and monocotyledons largely increased since 1980, while species of typical arable weed communities declined. The change in species number was not influenced by crop type or study design. Furthermore, neither geographic location nor precipitation of the study region had an influence on the outcome of the meta-analysis. This temporal development of the European arable flora suggests that conservation measures, such as ecological compensation areas like unsprayed field margins or wild-flower strips, may have helped to some extent to “slow” the decline in species numbers, but not in terms of typical arable weeds like corn-cockle or cornflower. Hence, more specific measures should be taken to stop this decline,

making sure that they are advantageous for rare arable species. Of course, it has to be taken into account that mainly threatened arable weeds and those plants beneficial for the farmer should be promoted. The growth of plants which bring a disadvantage for the production of agricultural goods should be prevented as much as possible.

Chapter 2

Since the introduction of arable farming more than 5000 years ago, a plant community evolved on arable fields that is adapted to frequent disturbances. These plants are mostly annual and their lifecycle is attuned to the rhythm of sowing an harvesting of the crop plant. Due to the intensification of agricultural practice during the last century, the diversity of these arable weeds has declined across Europe. A lot of those species are now on the Red List of threatened species. In Switzerland, no current study has been conducted on condition or change of the arable flora. To close that gap, vegetation surveys were conducted across Switzerland. They were based on historic studies of arable fields from 1927 to 1985 contained in the vegetation-database of Agroscope. The surveys were done at the same location as a historic one. Additionally, crop type (either cereal or root crop) and date had to correspond to the historic one. In 2011 and 2012, we re-surveyed 515 of these locations. If the current crop type corresponded with the historical one, we recorded all plant species on plots of $100m^2$ and estimated their abundance. Across all plots, species richness did not change considerably. However, mean number of species per plot declined by about 60% and mean ground cover of weeds by 90%. Most species decreased in frequency, but common species stayed abundant while rare species often disappeared. Species with increasing frequency were mostly neophytes (species introduced to Switzerland after AD 1500), grasses or species of high nutrient demand. Decreasing species were mostly species characteristic of traditionally managed weed communities. This decline in species number and frequency implicates that more explicit conservation measures have to be taken to ensure the persistence of rare arable weed species. This could be achieved by adapting the

catalogue of agri-environmental schemes or by establishing conservation fields as those in Biela (VS) or Brentjong (VS). Arable fields are a frequently and regularly disturbed habitat. Therefore, changes in the arable flora and thus the effect of conservation measures can be seen rapidly.

Chapter 3

Biodiversity can be separated into several parts the diversity of ecosystems, species and genes. In chapter 1 and 2 only the diversity of species was covered. To better understand the diversity of genes in the arable flora the phylogenetic relatedness was analysed. The analysis of the relatedness of species allows to fathom the relationship between environment and plant communities. In theory, plants growing in communities that are strongly influenced by competition between the plants, tend to be more distantly related. In contrast, species of communities that are strongly influenced by external effects, such as disturbances of the habitat, are more closely related. In this study the phylogenetic relatedness of plants of 232 historical and contemporary plots, respectively were analysed for plots on arable fields as well as on grassland across Switzerland. For each complete set of species of arable and grassland plots a pedigree was generated that showed the relatedness of the species. Based on this it was determined how closely related the species of one plot were in comparison to a randomly assembled plot. Thus, it was possible to compare the closeness of the relationship between the plots of the different time periods and communities. In fact, there was an increase of relatedness in the species from grassland to arable plots. Also on contemporary plots the plants were more closely related then on historic plots. Additionally, different traits of plant species were analysed in combination with relatedness of these species. The closer related the species in a plot were, the less diverse were the plant traits present. In contemporary plots with accordingly more closely related species grew a higher percentage of grass species, species with long living seeds and species typical for fertilized meadows. The closeness of the relationship of species in a plot on agricultural land can be an indicator of how much this community is influenced by humans without

having details on the actual agricultural practice. However, a high diversity of plant species and traits allow a community to adapt to a changing environment. Thus, the services that mankind relies on can be still be provided. This is a crucial point in the case of communities on agricultural land as they cover a third of the land masses of the earth and have to nourish all people.

Chapter 4

The developments of agricultural practice did not only result in high-input farming in the lowlands but also in the abandonment of fields in marginal profitable regions in the Swiss Alps. These fields had a rich arable flora to start with and the few still existing fields in these regions still belong to the most species rich in Switzerland. This is likely because most threatened arable weeds need a low amount of nutrients which are still given in these marginal profitable areas. As many arable weeds produce long-living seeds, such abandoned fields should have a high potential to promote those threatened plants if they are tilled again. To test this hypothesis, soil samples were taken on 38 former arable fields. They were located between 300 and 1730 m above sea level in the cantons Ticino and Grisons. In the centre and border of those abandoned fields 21 samples down to 20 cm were taken respectively. The samples of each area were pooled and afterwards the present plant-seeds washed out. The so gained seeds were sown in pots and put in a greenhouse to germinate for six months. Once a week, the seedlings were identified to species level and removed. Seedlings that could not be identified were put in a separate pot to grow until they were identifiable. A total of 119 plant species were identified, 96 in the border zone and 89 species in the centre of the former field. Of these 48 species were typical arable weeds. One of those (*Gypsophila muralis* L.)is mentioned on the Red List of threatened plant species of Switzerland. The three arable weed species that were re-found the most frequent were *Chenopodium album* L.*, Capsella bursa-pastoris* (L.) Medik. and *Viola arvensis* Murray. From the plants of the historic relevé 9.4% were re-found as viable seeds in the soil samples. Hence, the surveyed meadows had a small potential to promote threatened arable weeds if

tilled again. Probably, the sample size of 20 fields per region was too small to detect the seeds of threatened plants. It is likely that the fields were not tilled for too long and that therefore the seeds were not germinable anymore. If conservation fields should be established, the development of the arable weeds has to be surveyed. If no threatened species grow spontaneously after a few years it could be considered to sow the desired plants.

Zusammenfassung

Kapitel 1

In den letzten Jahrzehnten hat sich die landwirtschaftliche Praxis stark verändert. Die Bearbeitung der Felder wurde mechanisiert, künstlicher Dünger und Herbizide kamen zum Einsatz. Diese Intensivierung hat einerseits den Ertrag gesteigert, andererseits wurden Pflanzen und Tiere der Agrarlandschaft stark zurückgedrängt oder starben sogar aus. Daraufhin wurden in den 80er Jahren in Europa die Einführung von ökologischen Ausgleichsmassnahmen (z.B. Ackerschonstreifen, Brachen) beschlossen. Diese sollten die natürlichen Lebensgemeinschaften der Äcker wieder fördern. Um die Veränderung der Ackerbegleitpflanzen in einem grösseren Kontext aufzuzeigen, wurde anhand gesamteuropäischer Daten eine Meta-Analyse durchgeführt. Meta-Analysen vergleichen die Ergebnisse aller auffindbarer Studien, die zu einem Thema gemacht wurden. Dadurch soll eine sichere Aussage über den zugrunde liegenden Effekt gemacht werden können. Daher wurde nach europäischen Studien gesucht, welche historische mit gegenwärtigen Vegetationserhebungen auf Ackerflächen vergleichen. Das wurde mittels einer Internetrecherche gemacht. Aus 32 Studien welche unseren Kriterien entsprachen, konnten 53 Datensätze extrahiert werden. Die Studien verglichen Vegetationserhebungen von 1939 bis 2007. Über diese Datensätze gemittelt, sank die durchschnittliche Anzahl Arten pro Aufnahmefläche um 20%. Dies obwohl zwölf dieser Datensätze eine steigende Anzahl Arten pro Aufnahmefläche fanden. Studien die nach 1980 begonnen wurden, zeigten gemittelt eine steigende Anzahl Arten pro Aufnahmefläche. Die Veränderung der Anzahl Arten wurde weder von der angepflanzten Kultur, noch vom Design der ursprünglichen Studie beeinflusst. Auch die geographische Lage und Niederschlagsmenge in den Studienregionen hatten keinen Einfluss auf das Resultat der Meta-Analyse. Pflanzenarten, welche viel Nährstoff brauchen um zu wachsen, Neophyten und Einkeimblättrige nahmen seit 1980 zu. Im Gegenzug nahmen Arten der typischen Pflanzengemeinschaften der Äcker ab. Diese zeitliche Entwicklung der europäischen

Ackerbegleitflora weist darauf hin, dass die Schutzbemühungen, also zum Beispiel ökologischen Ausgleichsmassnahmen wie Ackerschonstreifen, die Abnahme der Vielfalt der Pflanzen auf Äckern verlangsamt haben könnte. Dies gilt jedoch nicht in Hinblick auf die typischen Ackerbegleiter wie Kornrade oder Kornblume. Es müssen also in Zukunft weitere Anstrengungen unternommen werden, um diesen Rückgang zu stoppen. Natürlich sollen dabei hauptsächlich gefährdete Ackerbegleitpflanzen und jene Arten, die für die Landwirte einen Nutzen bringen, gefördert werden. Das Wachstum von Pflanzen, welche für die Nahrungsmittelproduktion von Nachteil sind, sollten dabei möglichst vermieden werden.

Kapitel 2

Seit der Einführung des Ackerbaus vor über 5000 Jahren, hat sich auf den Äckern eine an viele Störungen angepasste Pflanzengesellschaft entwickelt. Diese Pflanzen sind meist einjährig und ihr Lebenszyklus ist dem Rhythmus von Saat und Ernte der Kulturpflanzen angeglichen. Durch die Intensivierung der Landwirtschaft in den letzten hundert Jahren hat die Vielfalt dieser Ackerbegleitpflanzen in ganz Europa abgenommen. In der Schweiz wurden jedoch keine aktuellen Studien zum Zustand und zur Veränderung der Ackerbegleitflora durchgeführt. Um diese Lücke zu füllen, wurde, basierend auf historischen Vegetationsaufnahmen von 1927 bis 1985 aus der Vegetationsdatenbank von Agroscope, auf Äcker in der ganzen Schweiz Vegetationserhebungen durchgeführt. Die Erhebungen wurden jeweils an derselben Stelle durchgeführt, an der schon eine historische Aufnahme gemacht worden war. Zusätzlich mussten auch die angebaute Kultur (Getreide oder Hackfrüchte) sowie das Datum der Erhebung mit der historischen übereinstimmen. In den Jahren 2011 und 2012 wurden insgesamt 515 Felder besucht. An 232 dieser Standorte wurde die selbe Kultur wie in der historischen Erhebung angebaut und daher konnte eine Vegetationserhebung gemacht werden. Dabei wurden auf 100m^2 die Pflanzenarten bestimmt und deren Bodenbedeckung geschätzt. Die Gesamtanzahl der Pflanzen über alle Aufnahmeflächen hat sich nicht gross verändert.

Die durchschnittliche Anzahl Arten pro Aufnahmefläche hat sich jedoch um ungefähr 60%, die Bodenbedeckung um über 90% verringert. Während die meisten Arten heutzutage weniger häufig vorkommen, sind doch die weit verbreiteten Arten immer noch die gleichen wie früher. Arten, die früher schon selten waren, sind in aktuellen Vegetationserhebungen jedoch meist nicht mehr zu finden. Die Arten welche weniger häufig vorkommen, waren Arten die charakteristisch sind für traditionell bewirtschaftete Ackerflächen. Es gibt aber auch Arten, die heute häufiger vorkommen als früher. Dies sind meist Gräser, Arten mit einem hohen Nährstoffbedürfnis oder Neophyten. Neophyten sind Pflanzenarten, die nach 1500 vom Menschen in die Schweiz gebracht wurden. Der Rückgang in Häufigkeit und durchschnittlicher Artenzahl von Ackerbegleitpflanzen weist darauf hin, dass grössere Anstrengungen zu deren Schutz getroffen werden müssen. Dies könnte durch eine Anpassung des Katalogs für Biodiversitäts-Förderflächen oder durch das Einrichten von Naturschutzäckern nach Vorbild von Biela (VS) oder Brentjong (VS) geschehen. Da Äcker ein häufig und regelmässig gestörter Lebensraum sind, können Veränderungen in der Ackerbegleitflora und dadurch der Effekt von Schutzmassnahmen schon nach kurzer Zeit festgestellt werden.

Kapitel 3

Biodiversität ist aus mehreren Teilen zusammengesetzt. Aus der Vielfalt der Ökosysteme, der Arten und der Gene. In Kapitel 1 und 2 wurde nur auf die Vielfalt der Arten eingegangen. Um die Vielfalt von Ackerbegleitpflanzen auf anderer Ebene besser einschätzen zu können, wurden deren verwandtschaftlichen Beziehungen analysiert. Die Analyse der Verwandtschaft von Arten ermöglichen es, die Beziehungen zwischen der Umwelt und den Pflanzengesellschaften besser zu ergründen. Die Theorie besagt, dass Pflanzen in Gesellschaften, die stark durch die Konkurrenz zwischen den Pflanzen geprägt sind, eher ferner miteinander verwandt sind. Dagegen sind Pflanzen in Gesellschaften, die stark durch äussere Einflüsse wie zum Beispiel Störungen des Lebensraumes geprägt sind, näher verwandt. In dieser Studie wurden die verwandtschaftlichen Verhältnisse von je

232 historischen und gegenwärtigen Erhebungen von Ackerpflanzen, sowie je 232 historischen und gegenwärtigen Vegetationserhebungen auf Grasland in der Schweiz angeschaut. Für die gesamte Artenliste der Äcker und Wiesen wurde jeweils ein Stammbaum erstellt, der die Verwandtschaft der Pflanzen aufzeigt. Darauf basierend wurde ermittelt, wie nahe verwandt die Arten der einzelnen Erhebungen im Vergleich zu einer zufällig zusammengestellten Erhebung waren. Dadurch konnte berechnet werden, ob sich die Pflanzenarten der Erhebungen der beiden Zeitperioden und Gesellschaften in ihrer verwandtschaftlichen Nähe unterscheiden. Tatsächlich fand sich eine Zunahme der Verwandtschaft von den Graslanderhebungen zu den Ackererhebungen. Auch von den historischen zu den gegenwärtigen Erhebungen nahm die Verwandtschaft der Arten zu. Zusätzlich wurden diverse Eigenschaften von Pflanzenarten im Zusammenhang mit der Verwandtschaft analysiert. Je näher verwandt die Arten in einer Erhebung waren, desto weniger vielfältig waren die vertretenden Pflanzeneigenschaften. In jüngeren Erhebungen, mit entsprechend näher verwandten Arten, kommen prozentual mehr Grasarten, Arten mit langlebigen Samen sowie Arten gedüngten Graslands vor. Die Nähe der Verwandtschaft der Arten einer Erhebung in landwirtschaftlichen Pflanzengesellschaften kann als Index genommen werden, wie stark die Gesellschaft durch den Menschen beeinflusst wird, ohne genaue Angaben über die Art der Bewirtschaftung haben zu müssen. Eine grosse Vielfalt an Pflanzen, Arten und Eigenschaften, ermöglichen einer Lebensgemeinschaft aber, sich einer sich verändernden Umwelt anzupassen. Dadurch können Leistungen von denen die Menschheit profitiert weiter erbracht werden. Dies ist gerade für die Lebensgemeinschaften der landwirtschaftlichen Flächen zentral, machen diese Flächen doch über einen Drittel der festen Erdoberfläche aus und müssen alle Menschen ernähren.

Kapitel 4

Die Entwicklung in der landwirtschaftlichen Praxis hatte nicht nur eine Intensivierung der Ackerflächen im Flachland nach sich gezogen, sondern auch zu einer Aufgabe von Feldern in den

Grenzertragsregionen der Alpen geführt. Diese Äcker hatten schon zu früheren Zeiten eine reiche Ackerbegleitflora und die wenigen, heute noch existierenden Felder in diesen Regionen gehören immer noch zu den artenreichsten der Schweiz. Dies wohl, weil die gefährdeten Ackerbegleitarten auf niedrige Nährstoffgehalte angewiesen sind welche auf diesen Grenzertragsflächen noch vorhanden sind. Da viele Ackerbegleitpflanzen langlebige Samen produzieren, sollten solche aufgegebenen Äcker ein hohes Potential haben um die gefährdete Ackerbegleitflora zu fördern wenn sie erneut beackert werden. Um diese Hypothese zu überprüfen, wurden auf 40 ehemaligen Ackerstandorten Bodenproben genommen. Die Standorte befinden sich zwischen 300 und 1730m.ü. M in den Kantonen Tessin und Graubünden. Je 21 Bohrungen bis auf 20cm Tiefe wurden im Zentrum sowie im Randbereich des ehemaligen Ackers entnommen. Die Proben eines Bereichs wurden zusammengelegt und anschliessend die enthaltenen Pflanzensamen ausgewaschen. Die so gewonnenen Samen wurden in Töpfe gesät und über sechs Monate im Gewächshaus keimen gelassen. Einmal pro Woche wurden Keimlinge auf die Art bestimmt und anschliessend entfernt. Nicht bestimmbare Arten wurden in einem separaten Topf weiter wachsen gelassen, bis sie bestimmt werden konnten. Insgesamt wurden 119 Pflanzenarten bestimmt, 96 im Randbereich und 89 Arten im Zentrum des ehemaligen Ackers. Davon waren 48 Arten typische Ackerbegleitpflanzen. Nur eine dieser Arten (*Gypsophila muralis* L.) steht auf der Roten Liste der gefährdeten Pflanzenarten der Schweiz. Die durchschnittliche Anzahl Ackerarten pro Aufnahmefläche war kleiner je höher am Berg die Parzelle lag. Die drei am häufigsten wiedergefundenen Arten waren *Chenopodium album* L.*, Capsella bursa-pastoris* (L.) Medik. und *Viola arvensis* Murray. Von den Pflanzen der historischen Vegetationsaufnahmen waren durchschnittlich 9.4% als keimfähige Samen in den Bodenproben vorhanden. Die untersuchten Wiesen haben also ein sehr kleines Potential gefährdete Ackerbegleitpflanzen zu fördern falls sie wieder umgebrochen werden. Eventuell war die Probegrösse von 20 Feldern pro Region zu gering um seltene Pflanzen zu finden. Es könnte jedoch auch sein, dass die Felder schon zu lange nicht mehr geackert wurden und die meisten Samen schon

nicht mehr keimfähig sind. Falls Naturschutz-Äcker eingerichtet werden sollten, müsste nach dem ersten Umbruch die Entwicklung der Ackerbegleitpflanzen beobachtet werden, und falls spontan keine seltenen Arten wachsen nach ein paar Jahren eventuell mit einer Saatmischung nachgeholfen werden.

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Employed as PhD-student at the Research station Agroscope Reckenholz-Tänikon ART since 01.01.2011

Work experience

01/2009 – 12/2011	Scientific researcher at Research Station Agroscope Reckenholz-Tänikon ART, vegetation database, vegetation surveys, orthopteran surveys
03/2008 – 12/2008	Internship at Research Station Agroscope Reckenholz-Tänikon ART
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Professional activities during Ph.D. studies

Teaching assistance	Biology undergrad courses BIO233 and 301 (Pflanzen und Lebensräume der Alpen, Vertiefung der Kenntnis einheimischer Pflanzen) at University of Zurich
Seminar organization	Annual Symposium of the PhD Program in Sustainable Agriculture at Agroscope in 2013
Professional work	Vegetation survey for the project BioBio in 2012 Vegetation survey for the project Stöckmatt 2011 – 2014 Survey of ground beetles in floodplains 2011-2014 Analyses for “Operationalization of Agriculture-Related Environmental Objectives” at Agroscope

Voluntary activities

2003	Collaborator Swiss Amphibian Red List
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